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Diversity and Distribution of Plant Communities Related to Forest Fragment Size, Shape, Age, and Structure

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DIVERSITY AND DISTRIBUTION OF PLANT COMMUNITIES RELATED TO FOREST FRAGMENT SIZE, SHAPE, AGE, AND STRUCTURE

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ABSTRACT

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In the Midwest region of the United States, forested areas have been removed to make way for agriculture and development. In the southern Midwestern states, including Indiana, cultivated and pasture agriculture lands account for 80-90% of rural landscapes. The remaining forests have been fragmented into small, often privately owned, woodlots. Due to their size, these forests typically have a high edge to interior ratio, which creates a greater influence of the surrounding agricultural land matrix upon the forest itself. Fragmentation influences the species in these forests through the distance between, size, age since disturbance, and shape of the forest in addition to management. By quantifying the intensity of these factors on plant species, management strategies could be modified to improve the ecological function of the fragments.

The objectives of this study were: 1) to identify the relationships between forest fragment and environment factors; 2) to test that fragmentation theory is applicable to

forest patches surrounded by agricultural matrix; and 3) to compare forest fragmentation results in Northeast Indiana to previous studies.

I surveyed thirty forest fragments in Adams, Wells, and Allen Counties, Indiana, identifying plants to species in stratified 25 m^2 understory and midstory plots. Richness, Shannon Entropy Index, and coefficients of conservatism were used to quantify understory diversity of each forest. Factors tested included ecological (Floristic Quality Index (FQI), basal area, overstory richness and diversity, and selective harvest) and environmental (area, perimeter, perimeter: area ratio, canopy cover, soil moisture, forest age, distance to nearest neighbor). Regression analysis and nonmetric multidimensional scaling (NMDS) was used to quantify interactions of diversity and factors.

Forest fragment area positively influenced understory richness and FQI as well as midstory richness. Distance to nearest neighbor had a negative effect with midstory species space and neighbor count within 1 km radius showed negative relation. Low valued species (<7) count doubled with a decrease in forest neighbor count in 1 km while high value species (>7) had a 13% increase with more neighbors. A negative relationship with perimeter: area ratio was noted in the understory species space and midstory diversity and FQI. Intermediate disturbance had a direct positive relationship with midstory richness and FQI values. Intermediate disturbance altered forest age, overstory diversity, and canopy cover, each of which had direct influence on under and midstory richness and diversity.

Large forest fragments that are selectively harvested with some perimeter effect show the greatest amount of plant diversity. These results are comparable to other research done on forest fragments and island biogeography with regard to size and disturbance, but not distance, thus fragmentation principles are applicable to forest patches surrounded by an agriculture matrix in northeast Indiana.

LITERATURE REVIEW

Island Biogeography

Many factors affect the distribution of plants and animals across a heterogeneous landscape. The theory of island biogeography suggests that species richness is primarily determined by island size and isolation (MacArthur and Wilson 1963, 1967). Other factors including island shape, age, and history also determine species diversity.

Island biogeography is described as a nearby mainland with islands as areas of suitable habitat surrounded by habitat that is unsuitable for the species (MacArthur and Wilson 1963, 1967). This includes an island of land surrounded by uninhabitable water, habitable ponds surrounded by land, forests surrounded by managed agriculture, grassland surrounded by infrastructure, etc.

Typically, species diversity increases with an increase of island size (MacArthur and Wilson 1963, 1967). This species-area-relationship is the result of larger islands generally having a greater diversity of habitats, creating a potential increase of inhabiting species (Hannus and von Numers 2008; MacArthur and Wilson 1963, 1967; Stracey and Pimm 2009). The greater occurrence of niches in the environment leads to a variety in competition in all kingdoms of life. Additionally, larger islands present larger targets to potential colonists leaving the mainland (MacArthur and Wilson 1963, 1967). As population size increases with more habitable land on larger islands, the extinction rate would decrease, allowing for more species that would have become locally extinct on smaller islands (Stracey and Pimm 2009). Higher densities of would also allow greater attraction to conspecifics, providing an animal behavior aspect to patch-size sensitivity (Fletcher, R 2009).

Islands that are closer to the mainland often have a greater chance of colonizer dispersal success. With a shorter distance between mainland and island, dispersal barriers are reduced and more species are able to colonize compared to those with greater distance (Stracey and Pimm 2009). This is important when comparing islands to the mainland, which is the source of the species found on islands. Isolation level can be compared between islands themselves. Aggemyr and Cousins (2012) identified distance to mainland as not significantly correlated with species diversity in any model. Instead nearby islands were greater factors as species were more likely to use nearby islands as stepping stones for movement rather than emigrating straight from the mainland (Aggemyr and Cousins 2012).

Shape of an island is also a factor in determining diversity, as edge to interior ratios influence species location or occurrence (Liston 2011, Tanentzap *et al.* 2010, Wallenius *et al.* 2010). As island area increases at a constant shape, so too does the relative contribution of the edge habitat, resulting in edge environments influencing inner habitat (Fletcher *et al.* 2007). Edges of an island and inner area can be described as two different environments and often have different richness values (Gonzalez et al 2010).

Older islands typically have greater potential to have been colonized due to increased time available compared to younger islands (Aggemyr and Cousins 2012, Horsák *et al.* 2012). The history of an island also plays a key role in current diversity as past landscape configuration and management still may hold influence (Aggemyr and Cousins 2012). Past shape and perimeter to area ratio may still influence current resident species, particularly long-lived ones, creating remnant populations (Eriksson, 1996). Other species may live well after habitat alteration and then suddenly disappear, resulting in an 'extinction debt' (Tilman *et al.* 1994). History may bias results if not taken into consideration.

Fragmentation

Without a mainland, fragmentation studies may be used to compare small island-like environments. Fragmentation is a landscape-scale process in which habitat is lost and broken apart, creating smaller fragments that are isolated from each other by an environment matrix unlike the original (Wilcove *et al* 1986). Much research has been conducted considering the differences between continuous and fragmented landscapes, but these do not assess the full implications of fragmentation as they do not show the relationship between degree of fragmentation and diversity response (Fahrig 2003, Gonzalez *et al* 2010, Horsák *et al* 2012). The pattern of the habitat in the study area provides information on response (Fahrig 2003).

There are four primary effects of fragmentation on habitat pattern: 1) habitat extent is reduced, 2) habitat fragment number is increased, 3) habitat fragment size is decreased, and 4) fragment isolation is increased (Fahrig, 2003). These effects influence diversity differently and can result in studies looking at fragmentation as either habitat loss or changed. As these changes are not entirely exclusive, relationship and factor importance are needed for universal studies; for instance, examining if fewer, larger fragments with greater isolation have higher diversity than more, smaller fragments with less isolation (Fahrig, 2003).

In general, fragmentation is noted to have large negative effects on species richness, population abundance and distribution, and genetic diversity (Fahrig, 2003). Habitat loss has a negative effect on population growth rate, with declining global abundance predicted and alteration of species interactions and reduced breeding success, dispersal success, and specialist species richness shown (Donovan and Flather 2002, Fahrig 2003). Changes can be seen from the individual, population, and ecosystem level. These common responses to habitat fragmentation, however, are dependent on the species being observed and the availability of complementary resources in the new matrix (Haynes *et al* 2007). Species that are highly mobile (e.g. mammals, birds, insects, early-successional plants), generalist predators, and long-lived species often show positive relationships, differing from the normal response (Debinski and Holt 2000, Marshall and Storer 2006).

Forest Specific Fragmentation

In the Midwest region of the United States, wooded areas have been removed to make way for agriculture and settlement. In the southern states of the Midwest, including Indiana, cultivated and pasture agriculture lands account for 80-90% of rural landscapes (Table 1, Figure 1). The forests have been fragmented into woodlots that are small and often privately owned.

Major forest fragmentation within the Midwest was initiated by European colonization converting land for habitation. In the 21st Century, it is still a threat as human population is increasing (Ritters *et al.* 2012). Open land was created for industry, residence, and cultivation, separating and shrinking natural landscapes. Infrastructure such as roads, irrigation canals, and wide cultivated land can create barriers to dispersal for numerous species. Human activity, such as vehicles along a road, airplanes inadvertently carrying seeds, and creation of ditches can be used as a corridor for others, assisting in dispersing seeds or individuals from one area to another. Forest fragmentation may not just reduce biodiversity of the forest, but removal of forests that act as filters near streams may negatively affect water quality, including human drinking water supplies (EPA 2003). Continued fragmentation may also lead to deforestation, resulting in accelerated climate change by the release of carbon stored in trees (EPA 2003).

Succession

Succession is the predictable natural progression of species through time in a specific area. When observing forests, succession can be seen in four main stages of overstory growth: sapling-pole, young, mature, and climax (Martin and Gower 1996). During these stages, the replacement of tree species creates the conditions for the next stage, creating more stable communities that eventually reach a more stable equilibrium, thus there is more competition for resources and species richness is greater in the earlier stages with tolerant species eventually dominating the site in the climax stage (Martin and Gower 1996).

Interactions between species in the over and understory influence canopy composition (Quigley and Platt 1996). Understory composition influences the spatial pattern of the overstory trees through survival and growth of juvenile trees in gap areas, and subsequent recruitment of trees into larger size classes (Platt and Schwartz 1990). This vertical stratification within deciduous forests in the northern United States is prompted by seasonality in addition to canopy gap formation (Quigley and Platt 2003). With deciduous forests, the change in seasons provides temporary overstory gap. This seasonal openness permits woody and herbaceous plants in each strata to grow without the extensive gap formation created from tree removal, allowing for persistent understory plant populations (Quigley and Platt 2003).

The longevity of woody plant species, particularly overstory trees, can illustrate the influence of past management and landscape configuration of the forest fragment, biasing studies that seek an understanding of current fragment influence (Cousins, 2009). Diversity of herbaceous species found in the understory is less influenced by historical management and landscape features as their generation time is far shorter, allowing for more current fragmentation influence to be noted.

Dispersal

For plants, the potential for dispersal is limited by the mechanism that they use. Understanding seed dispersal is essential when determining spatial patterns of plants (Talavera, *et al*. 2012). All species of plant are at the mercy of self-dispersal, animals, wind, or water to transport the seeds. If these mechanisms are affected by fragmentation of forests, then so is dispersal. For instance, dispersal by birds was not significantly different between edge and interior of forest fragments, while those that used wind and other animals show higher counts in the edge (Gonzalez *et al* 2010). Life history traits of plants that are most negatively affected by forest fragmentation included clonal forest specialist species that had few and heavy diaspores without dispersal structures, small and short lived seeds, and insect pollinators (Kolb and Diekmann 2005).

Vascular plants often have dispersal limitations that impact habitat specialist richness (Horsák *et al.* 2012). Due to this, older fragments would have greater richness as younger sites may not have enough time for appropriate colonist recruitment (Cristofoli *et al.* 2010). However, with an increase of fragment age, species dispersal ability decreases for habitat specialists (Horsák *et al.* 2012).

Fragment isolation results in loss of diaspores in uninhabitable terrain (Cody and Overton 1996).This drives selection against dispersal rate, creating older populations with low dispersability (Oliverieri and Gouyon 1985). Disturbance produces unpredictable environments in which dispersal polymorphism with some seeds distantly dispersed is advantageous (Snyder 2011). This could be utilized in forest fragments, which are more stable than other environments, such as rocky turf and grasslands, and have lower dispersibility (Talavera *et al.* 2012).

Edge Effects

Due to their small size, forest fragments often have a high edge to interior ratio, which creates a greater influence of the surrounding agricultural land matrix upon the forest (Gonzalez *et al.* 2010). As fragment size decrease, the ratio of forest edge to area increases, creating a greater influence on edge on the habitat, with smallest habitats consisting of only edge (Ewers *et al.* 2007).

Recruitment of native species is reduced with greater edge effects, but increased with non-natives (Bruna 2002, With 2002). Non-native species invasability is associated with a decrease in fragment size, with greater edge to area ratio (With 2002). Forest patches in human-modified landscapes are particularly susceptible to non-native species invasion through increased propagule pressure (Borgmann and Rodewald 2005, Tanentzap and Bazely 2009). Non-native species are commonly introduced in these areas by human horticulture, agriculture, and settlement (Mack and Lonsdale 2001).

Additions of corridors to increase patch connectivity would increase native richness greater than non-native richness (Tanzentzap *et al.* 2010).

The shape of the fragment will increase the effect of edge with increased perimeter, creating synergistic interactions between edge and area (Ewers *et al.* 2007). The strength of the edge effect changes exponentially with increasing fragment area; small fragments have little to no effect as they lack forest core like conditions maintain certain species that prefer forested habitat (Ewers *et al.* 2007). Larger forest fragments have a distinct difference in edge and interior habitat, with species richness having a steeper increase in the edge and thus the edge effect should be taken into account with studies (Gonzalez *et al.* 2010). The surrounding matrix varies the strength of the edge effect with greater contrast in vegetation generally resulting in greater effect (Hartley and Hunter 1998, Ries *et al.* 2004). This has been noted with height of vegetation and vegetation density, with different species effecting dissimilarly (Ries *et al.* 2004).

Management of Forests

Forest management has become of recent concern as forests have become highly fragmented and often privately owned, leading to varied management practices (Trani *et al.* 2001). Competition of species is affected, changing richness of native and non-native species as well as levels of competitors (Collins 1995, Tanentzap *et al.* 2010). In the United States, legislation was passed in the late twentieth century to provide monetary support to help compensate biodiversity loss, but with only so much effect (USDA).

Native and Non-native Species

Each plant species is not directly influenced by fragmentation in the same way. By quantifying the intensity of environmental and geographical factors on plant species, management strategies could be modified to improve the ecological function of the forest fragments. Ecosystem-based management may provide the required habitat for most species, maintaining diversity (Hunter 1999, Lindenmayer *et al*. 2006).

Invasive non-native species potentially impact native species, thus their reduction is a key aspect of several management strategies (Tanentzap *et al*. 2010). In forests in Ontario, Canada, non-native species richness was significantly correlated with mean shape index, a ratio of forest edge to area, and positively correlated with mean distance to nearest neighbor patch (Tanentzap *et al.* 2010). As native plant dispersal is poor, management efforts to maximize connectivity through corridors would benefit native populations (Tanentzap *et al.* 2010).

Intermediate Disturbance

Forests in eastern United States have shown a decline in young forests due to habitat loss and maturing of forests caused by the lack of management on privately owned land (Trani *et al.* 2001). Although management measures including selective harvesting, effective fires suppression, and abandonment of agricultural fields have been performed, the current distribution of young forests is below what is needed to sustain desired population levels of some wildlife (Askins 2001, Trani *et al.* 2001).

The intermediate disturbance theory suggests that richness will be highest following occurrences of mid-levels of disturbance (Connell 1978). This is due to a trade-off of tolerance to disturbance and ability to compete, with superior competitors assumed to be most susceptible to disturbance (Collins 1995). Richness decreases if disturbance is too frequent, as intolerant plants become locally extinct or colonization cannot occur, and too infrequent, as dominant species overwhelm the weaker competitors (Collins *et al.* 1995). High richness following intermediate disturbance has been noted in forest, stream, grassland, and marine communities (Collins *et al.* 1995, Dial and Roughgarden 1998, Townsend *et al.* 1997).

To improve richness in the remaining forests, management may include emulation of natural disturbance (END), providing landscape patterns known to renew and maintain critical processes and habitat for conserving diversity (Long 2009). END allows for desired ecological goods and services to be maintained and reduces the probability of becoming an undesirable state (Drever *et al*. 2006). Selective forest harvesting creates mid-level disturbance, changing the succession process through canopy gap formation, soil turnover, and seed dispersal, creating forests that have young trees that are in earlier succession stages (Trani *et al.* 2001),

Private Ownership

Approximately forty-five percent of forestland in the United States is owned by nonindustrial owners (USDA Forest Service 2013). Decline in early successional forests is promoted as individual landowners change the forest characteristics and resources available through lack of management. This effect is amplified with several individuals owning sections of one forest as there is little opportunity for forest management and thus disturbance (Trani *et al.* 2001). As young forests provide quality habitats for several species, conservation is of concern as loss of these species may be seen (Hunter *et al.* 2001).

Within the latter half of the 20th century, environmental awareness increased through passage of the Endangered Species Act and Water Acts in addition to the establishment of the Environmental Protection Agency (Sharitz *et al.* 1992). Land owners could become members of the Forest Stewardship Program, receive financial assistance, and obtain lumber with selective cuts (Department of Environmental Conservation, USDA). Owners may receive property tax breaks, forestry literature, and free forester inspections by enrolling their land as a classified forest. In Indiana, the Classified Forest Program protects private forests approximately 4 ha (10 acres) or larger that support native or planted trees and that serves the purposes of timber, wildlife, protection of watershed, or control of erosion (IN.gov). Through the Classified Forest Act, measures have been taken to require members to use minimum good standards of timber management and follow an approved plan (IN.gov). However, management of smaller forests or those not part of government programs is unpredictable.

Table 1. Number, area of forest patches, and percent of land over in forest and agriculture in Adams, Allen, and Wells Counties, Indiana, as well as the southeast portion of Allen County based on 2001 National Land Cover Data.

County	Number Forest Patches	Total Area Forest (ha)	Mean Forest Patch Area (ha)	County in Forest (%)	County in Agriculture (%)
Adams	2040	4162.98	2.04 (3.75)	4.73	85.85
Allen	7681	14997.11	1.95 (5.76)	8.77	65.32
SE Allen	556	1783.52	3.21 (5.66)	6.06	85.75
Wells	2601	5618.21	2.16 (4.89)	5.86	86.42

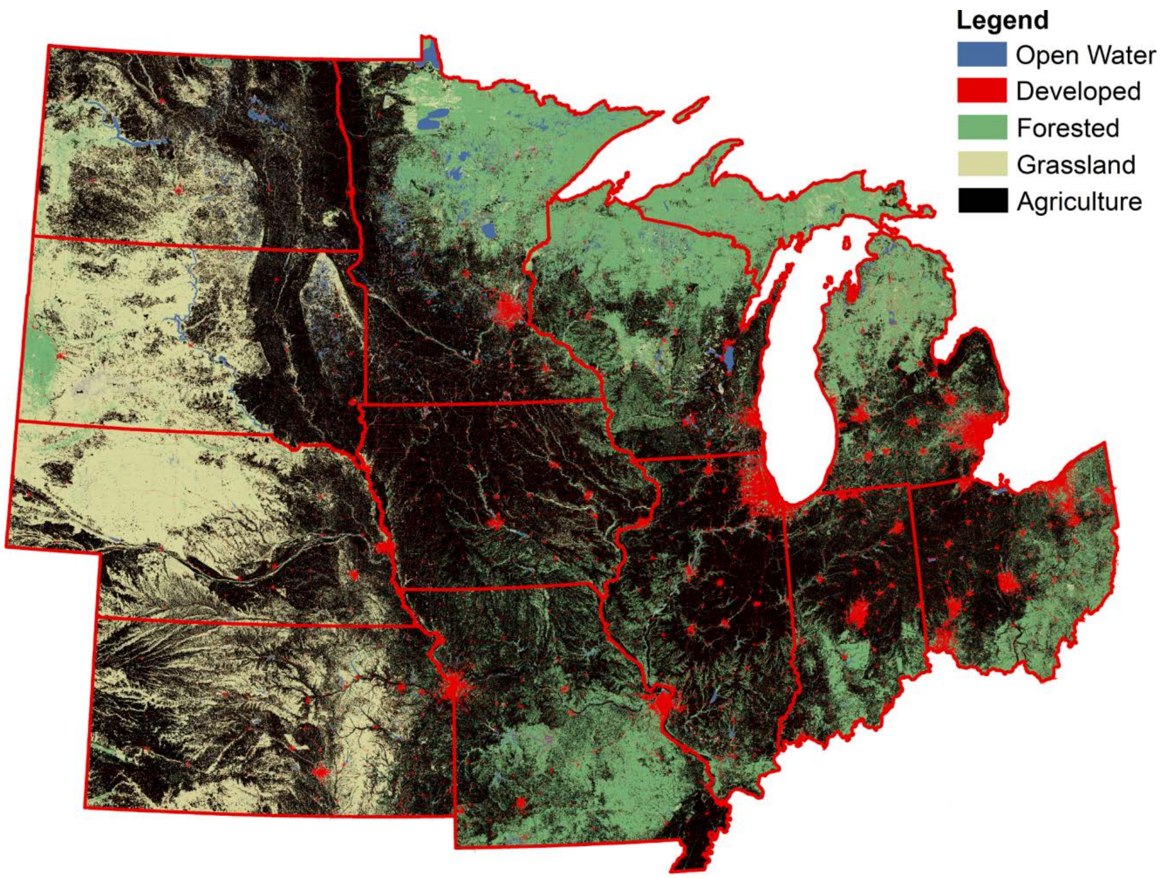

Figure 1. Simplified land use for Midwestern states (NLCD 2006).

INTRODUCTION

Through the process of habitat fragmentation species become isolated, landscape variation is modified, and environmental conditions are segregated. There are four primary effects of fragmentation on habitat pattern: 1) habitat amount is reduced, 2) habitat fragment number is increased, 3) habitat fragment size is decreased, and 4) fragment isolation is increased (Fahrig, 2003). Habitat loss has a negative effect on population growth rate, with declining global abundance predicted and altered species interactions and reduced breeding success, dispersal success, and specialist species richness shown (Donovan and Flather 2002, Fahrig 2003). Changes can be seen from the individual, population, and ecosystem level. Species that are highly mobile (e.g. mammals, birds, insects, early-successional plants), generalist predators, and long-lived species often differ from the normal response (Debinski and Holt 2000, Marshall and Storer 2006).

Many factors affect the occurrence of abundance of plants and animals across a heterogeneous landscape. Species variation increases with an increase of land size and age as well as a decrease of distance from one fragment to another. Larger fragments generally have a greater diversity of habitats, resulting in a potential increase of inhabiting species (Hannus and von Numers 2008). The shape of the fragment is also a factor, as high edge to interior ratios influence corridors for species movement, thus colonization rates (Liston 2011, Tanentzap *et al.* 2010, Wallenius *et al.* 2010). The older the fragment, the greater potential there is for colonization due to increased time compared to younger fragments (Aggemyr and Cousins 2012, Horsák *et al.* 2012). Fragments that are closer to each other have a greater chance of colonizer dispersal success. With a shorter distance, the barrier of separation lessens and a greater number of species are able to disperse compared to those with a greater distance (Stracey and Pimm 2009).

In the Midwest region of the United States, wooded areas have been removed to make way for agriculture and settlement lands. In the southern states, including Indiana, cultivated and pasture agriculture lands account for 80-90% of rural landscapes (Figures 1, 2). Forests have been fragmented into woodlots that are small and often privately owned. Due to their size, the forest fragments often have a high edge to interior ratio, which creates a greater influence of the surrounding agricultural land matrix upon the forest itself (Ewers *et al.* 2007, Gonzalez *et al.* 2010, Tanzentrap *et al.* 2010). Forest fragmentation influences the species in these forest fragments through the distance between, size, age, and shape of the forest. Each plant species, however, is not directly influenced in the same way.

Forests as an ecosystem behave uniquely to fragmentation. Succession is the predictable natural progression of species through time in a specific area and is grouped into stages of species replacement, with earlier stages having greater competition and species richness (Martin and Gower 1996). Fragmentation may alter the successional pathway, and thus species diversity. For plants, the potential for dispersal is limited by the mechanism that they use. Understanding seed dispersal is essential when determining spatial patterns of plants (Talavera, *et al*. 2012). All species of plant are at the mercy of self-dispersal, animals, wind, or water to transport the seeds. If these mechanisms are affected by fragmentation of forests, then so is dispersal. By quantifying the intensity of these factors on plant species, management strategies could be modified to improve the ecological function of the forest fragments.

The objectives of this study were: 1) to identify the relationships between forest fragment size, shape, isolation level, age, human influence, and connection to other forests and the under and midstory plant communities; 2) to test the hypothesis that fragmentation principles are applicable to forest fragments surrounded by agricultural matrix; and 3) to compare forest fragmentation results in Northeast Indiana to previous studies.

METHODS

Suitable forest fragments were identified in the study region of northeast Indiana, specifically in Adams, east Wells, and southeast Allen Counties. These counties were historically dominated by hardwood forests that have been converted into row crop and pasture fields, creating fragmented and isolated forests (Figure 2). Additionally, these portions of the counties have relatively sparse populations (0.34 people/ha). Properties were identified using aerial photography to locate forest fragments and county plat maps to identify land owners. Initial contact with landowners was made via telephone to discuss the project. After gaining permission from landowners, plant surveys were conducted within each forest and forest metrics related to the physical structure were measured during Summer 2013. Species diversity relationships were identified though measurements of evenness and richness as well as use of the Shannon Entropy Index ($H' = \Sigma p_i \ln p_i$, where p_i is the proportion of the *i*th species within the forest).

Field Data Collection

A random, stratified sample of suitable forest fragments was determined by placing available fragments into size classes (< 5, 5 < 10, 10 < 15, > 15 ha). Thirty forest fragments were sampled from June to August 2013 from each with the goal to maximize variability of area. Forest fragment selection was prioritized in north Adams, northeast Wells, and southeast Allen counties (Figure 2).

Plant surveys were conducted in each identified forest fragment. Surveys consisted of stratified, random points within the forests. Plots were randomly selected from a 25.6 m spaced grid including a 25.6 m buffer in ArcMap (version 10.1, ESRI Inc., Redlands, CA). The minimum number of plots was arbitrarily derived from the size class of the forest, or in some cases the area of forest permitted to study with forest fragment size classes of < 5, 5 < 10, 10 < 15, and > 15 ha having 4, 6, 8, and 12 plots respectively. All individual understory herbaceous and woody plants (<2 m height) were identified to species and counted within a 25 m^2 square plot (5 m x 5 m). In this same plot, mid-story species (≥2 m height and <8 cm diameter at breast height [dbh]) were counted, identified to species, and measured. All overstory tree individuals (≥ 8 cm dbh) were identified to species and dbh measured within a 500 m^2 circular plot (12.62 m radius) centered on the under and midstory plots. Physical environmental characteristics that were measured within each understory survey plot included soil moisture (FieldScout TDR meter, Specrum Technologies, Inc., Aurora, IL) and forest canopy cover (concave spherical densitometer, Forestry Suppliers, Jackson, MS). Lastly, to assist in identifying the age of the forest fragment and potential fire or management history, an increment borer was used to core the largest tree within each overstory plot, excluding high-value hardwood species identified by the land owner. Standard dendrochronology techniques were used to age trees and identify gap release and other changes in forest structure.

Forest size, shape, distance to nearest forest fragment in each cardinal direction, and number of forests within a 1 km and 2 km radius as a surrogate for isolation were calculated for each forest fragment using ArcMap. Ratio of perimeter to area was also calculated.

Data Analysis

By combining the field data with geographic information data, an interpretation of the spatial distribution of plant species in relation to geographic patterns of shape, size, isolation level, isolation age, and structure was created with regard to previous management of forests. This analysis identified relationships between species, assisting in understanding ecological interactions across the landscape.

For each of the thirty forest fragments, under and midstory species, richness, evenness, and diversity using the Shannon Entropy Index was calculated (Hayek and Buzas 1997). Average coefficient of conservatism (C) and floristic quality index (FQI) were calculated for each forest, taking into account native species in Indiana and their degree of tolerance to disturbance (Rothrock 2004). Coefficients for each native plant species range from 0 to 10 with low numbers indicative of species highly tolerant of disturbance and high numbers associated with species highly intolerant of disturbance and restricted to pre-settlement-like communities (Rothrock 2004). The FQI (Mean C * √N where C is the coefficient of conservation for each native species identified in the forest fragment and N is the total number of native species in the study area) included a richness component with high FQI numbers indicating high floristic integrity and low levels of disturbance to the fragment (Rothrock 2004).

Prior to data collection, communication occurred with the landowners regarding short- and long-term management goals for each forest. Forests that were noted to have been selectively harvested in the last 20 years were categorically marked as harvested. This included six of the thirty forests, two owned by forest products companies and four by private owners at the time of the harvest. Harvested versus non-harvested forest fragments were used as an environmental variable in calculations. T-tests were performed comparing harvested and non-harvested forests to forest factors (version 16.2.4, MiniTab Inc, State College, Pennsylvania). Factors examined were broken into two groups: ecological factors included FQI, basal area, overstory richness and diversity, and selective harvest; environmental factors included area, perimeter, perimeter:area ratio, canopy cover, soil moisture, forest age, distance to nearest neighbor (average of distance of closest forest in each cardinal direction), and forest neighbor counts in 1 km and 2 km radii.

Comparison between counties and environmental/ecological factors was performed using one-way ANOVA ($\alpha = 0.05$) in MiniTab (version 16.2.4, MiniTab Inc, State College, PA). Nonmetric multidimensional scaling (NMDS) ordination was performed using understory and midstory species counts at the forest level using R (version 3.0.2, The R Foundation for Statistical Computing vegan package). Stress levels were calculated for analysis of forest space by county.

Plant diversity analysis consisted of standard statistical analysis comparing data between forest fragments. Multiple regression was used to test for relationships between understory and midstory species richness and environmental variables using reverse variable selection to remove variables that added the least information to the model ($\alpha = 0.05$) with collinear variables removed when necessary. Similar regressions was performed for under and midstory species diversity and FQI as well as understory species in the categories of native, non-native, herbaceous, and woody. Multiple regression analyses were conducted using MiniTab (version 16.2.4, MiniTab Inc, State College, PA).

NMDS ordination was performed for species level analysis, creating species space of species abundance of the under and midstory. Environmental variable influence on species distribution with a cutoff of $R^2 = 0.2$ with vectors was additionally created for analysis using R (version 3.0.2, The R Foundation for Statistical Computing vegan package).

Conservatism of species was analyzed using coefficents of conservatism as defined by Rothrock (2004). Species were separated into low and high C values (<7 and $\geq$7 respectively). Separation of values was determined using Rothrock's (2004) designations, in which species are placed on a scale of 0-10 on how confidently the plant was taken from a remnant natural plant community, with 1-3 not confident, 4-6 typically found with remnant communities but disturbance tolerant, 7-8 species found in high-quality remnants, and 9-10 species restricted to areas with little post-settlement trauma. Multiple regression with reverse variable selection determined significant factors ($\alpha = 0.05$). Significant values were used in CoKriging spatial analysis (ArcMap version 10.1, ESRI, Redlands, CA). Plant species count per survey area was compared against high and low environment and ecological factors, with high values including those in the top third (10 forests) and low the bottom third (20 forests) for each individual factor. Survey area was calculated by number of plots in forest multiplied by $25m^2$. Values were compared using G-statistic with ($\alpha = 0.05$).

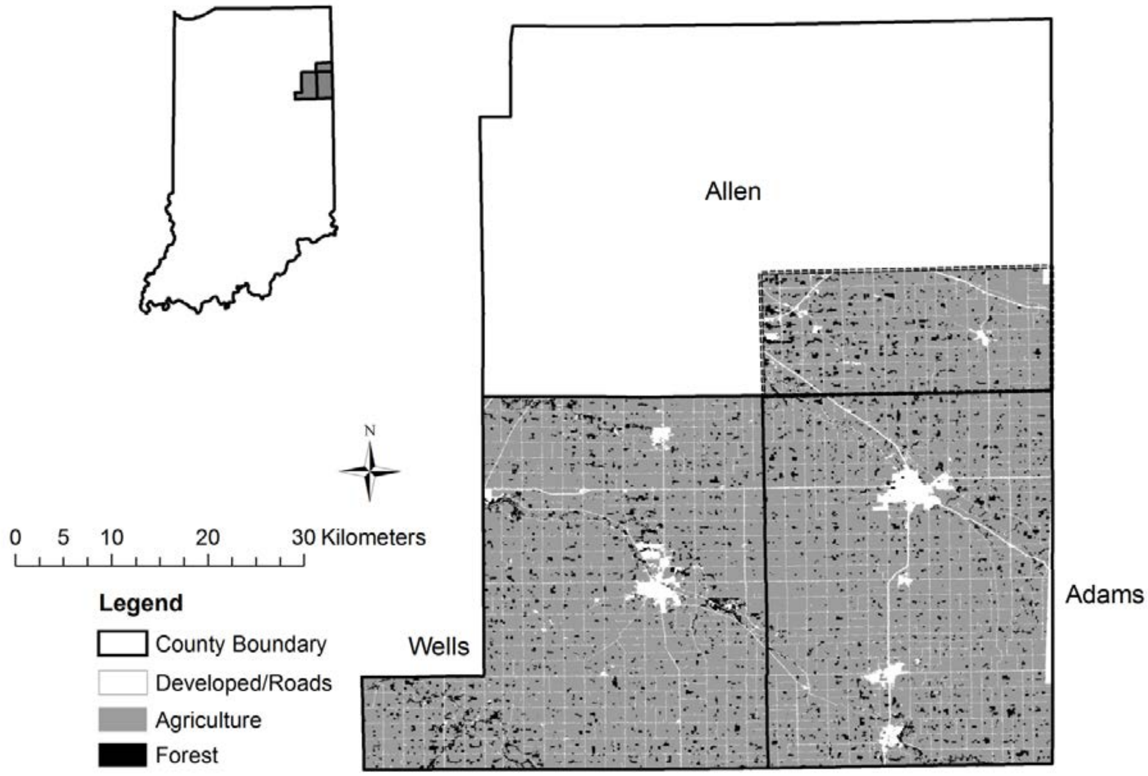

Figure 2. Simplified land use cover data from Adams, Wells, and southeastern Allen (dashed outline) Counties, Indiana. Data source: U.S. Geological Survey (NLCD, 2006).

RESULTS

A total of 89 understory species were encountered within the 30 forests surveyed, occurring in 44 families (Appendix C). Additionally, a total of 25 midstory species were encountered within the forests, occurring in 16 families (Appendix D).

Study Forest Patterns

One-way ANOVA analysis was performed between counties (Adams, Allen, and Wells) to compare ecological and environmental factors. Of environmental factors, canopy cover and neighbor count in 2 km radius resulted in significant difference between Adams and Wells Counties (Table 2). Non-metric multidimensional scaling ordination analysis of site relationships between counties was performed. For understory species relationship, there was substantial overlap in species richness with few forest fragments found in Adams County barely outside this overlap with a final stress = 0.23 (Figure 3, 5A). Overlap was even greater for midstory species between counties with a final stress = 0.19 (Figure 4, 5B).

Relationships between proportion of species encountered and number of plots surveyed was analyzed with each size class. For both understory and midstory species, species area curves began to approach an asymptote at 4 survey plots at approximately

80% species encountered for each size class (Figure 6, 7). This suggests that an adequate number of plots were surveyed in order to encounter the majority of species within the forests.

Forests that had been selectively harvested within the last 20 were compared with those forests not harvested with forest factors. Differences were noted with midstory species richness and diversity as well as understory species diversity (Table 3). The harvested forests were spread distantly within the study area (mean forest distance: Adams = 904.8 m, Allen = 2168.8 m, Wells = 574.2 m, Figure 8).

Regression Analysis

Relationships between understory species and environmental factors were identified in multiple regression models (Table 4). Understory richness displayed increases in forest area and overstory diversity (Table 4). Little understory richness was noted with low overstory diversity, despite range in forest area (Table 4). Diversity was negatively influenced by forest fragment age and 1 km buffer with positive influence of perimeter and canopy cover (Table 4). Understory FQI was positively influenced by area and overstory diversity (Table 4).

Multiple regression of midstory species richness had a positive relationship with area, soil moisture, overstory diversity, and harvest as well as negative with perimeter (Table 4). Midstory diversity was found to be negatively influenced by the perimeter:area ratio and positively by overstory diversity and soil moisture (Table 4).

FQI was influenced positively by overstory diversity and harvest and negatively by perimeter:area ratio (Table 4).

Factor contribution to both native and non-native understory species was also calculated using reverse variable selection (Table 4). Non-native understory species showed a steep incline of positive relationship with area and negative with perimeter (Table 4,). Native species displayed negative relationship with the perimeter:area ratio (Table 4).

Multiple regression of understory woody species (Table 4) related negatively with perimeter:area ratio, forest age, and forests within a 1 km radius as well as positively with soil moisture and overstory diversity (Table 4). Understory herbaceous species showed positive relationship with perimeter and canopy cover, with high values constantly noted with high perimeter and with both low and high canopy cover (Table 4).

Ordination Analysis

For understory species ordination, vectors for FQI, moisture, perimeter:area ratio, canopy, and overstory diversity were included with a cut off of $\alpha=0.2$ (Table 5, Figure 9). Length and direction of the vector relates to the influence the vector has on the species. Majority of the species are equally influenced by the environmental factors, and thus are grouped centrally. Noted trends included perimeter:area ratio and moisture equally influencing all four oak species with *Quercus velutina* Lam. (Quve) the most influenced, then *Q. bicolor* Willd. (Qubi), *Q. rubra* (Qure), and *Q. alba* L. (Qual) influenced least. A small cluster of species was heavily influenced by both canopy and perimeter:area ratio including the *Rosaceae* family (Rofa), unidentifiable maple seedlings (Acsp), and *Populus grandidentata* Michx. seedlings (Pogr), all smaller woody species that were more likely to be found near the perimeter of forest fragments. FQI displayed the longest vector, thus had great influence on species space, including positive influence on *Solidago flexicaulis* L. (Sofl). Midstory species space resulted in vectors of distance, evenness, and canopy cover ($\alpha = 0.2$). Majority of species were negatively influenced by the factors (Table 6, Figure 16).

Conservatism Analysis

Analysis of conservatism of native plant species was performed for species with low (C <7) and high C values (C $\geq$7). Plant species found in the understory with C values/survey area (25 m^2 x number of plots surveyed) were compared against ecological and environmental factors using multiple regression. No factors were significantly related to species with high C values. Species with low C values were minimally positively related with perimeter and basal area and negatively related with forest age (<7C = 7.20 + 0.000992 Perimeter - 0.0740 Age + 0.0385 Basal Area, $F = 4.84$, df = 2,27, $p = 0.008$, $R^2 = 0.61$). CoKriging analysis was performed with low C value counts/survey area and perimeter and basal area as parameters, displaying high probability of low C-value species in the north and west of Adams County and East Wells County (Figure 11). G-statistics were also performed with all environmental and ecological factors against high and low C valued plant species. Increased neighbor count within 1 km radii displayed a two-fold decrease in low level species and a 13% increase in high level species. Increase in overstory richness decreased low level species by 10% as well as a two-fold increase in high level species (Table 7). A decrease in overstory diversity showed a three-fold increase with low level species with no change in high level species (Table 8). CoKriging analysis was performed with high C value counts/survey area and overstory richness, diversity, and neighbor count within 1 km, displaying high probability of encountering high C value species in north, west Adams County into Allen County (Figure 12).

Table 2. One-Way ANOVA results for forest fragments by county (Adams, Allen, Wells) for each environmental and ecological factor. Asterisk (*) indicates significant differences.

Factor	$F_{2,27}$	P
Understory Richness	0.18	0.835
Understory Diversity	0.26	0.772
Understory FQI	0.41	0.667
Forest Area	0.41	0.666
Forest Perimeter	0.26	0.776
Perimeter/Area	0.23	0.794
Canopy Cover	0.49	0.001*
Soil Moisture	0.49	0.617
Forest Age	0.50	0.614
Basal Area	0.25	0.777
Overstory Richness	0.77	0.472
Overstory Diversity	0.12	0.883
Neighbor Distance	1.52	0.238
2 km Radii	4.02	0.030*
1 km Radii	1.26	0.299
Selective Harvest	0.94	0.403

Tukey's HSD identified differences between Adams and Wells.

Table 3. One-tailed t-test comparing selective harvested forest fragments against environmental and ecological factors. Asterisk (*) indicates significant differences with harvested forests greater than unharvested. MS = midstory, OS = overstory, US = understory.

Factor	$t_{(1),28}$	P
1 km Radii	-0.88	0.807
2 km Radii	-0.28	0.610
Basal Area	-0.84	0.796
Canopy Cover	0.37	0.358
Forest Age	-1.17	0.874
Forest Area	1.66	0.054
MS Richness	1.95	0.031*
MS Diversity	2.06	0.025*
Neighbor Distance	-0.50	0.691
OS Diversity	0.68	0.250
OS Richness	1.78	0.043*
Forest P/A	-1.00	0.837
Forest Perimeter	1.53	0.069
Soil Moisture	0.48	0.319
US Diversity	1.65	0.055
US FQI	0.68	0.251
US Richness	1.86	0.036*

Table 4. Regression analysis for variables and environmental/ecological factors with p < 0.05. Asterisk (*) indicates significant differences. MS = midstory, OS = overstory, US = understory.

Equation	$F_{2,27}$	R^2	**P**
US Richness = 14.5 + 0.410 Area + 8.74 OS Diversity	17.07	0.56	<0.001*
US Diversity = 0.560 + 0.000217 Perimeter + 0.0259 Canopy Cover - 0.00966 Age - 0.0578 1Km_Buffer	6.73	0.52	0.001*
US FQI = 12.9 + 0.152 Area + 4.18 OS Diversity	10.46	0.40	<0.001*
MS Richness = - 2.47 + 0.376 Area - 0.00235 Perimeter + 0.0493 Soil Moisture + 2.60 OS Diversity + 2.80 Harvest	22.90	0.79	<0.001*
MS Diversity = 0.379 - 0.00384 P/A + 0.00884 Soil Moisture + 0.584 OS Diversity	15.09	0.59	<0.001*
MS FQI = 8.54 - 0.0293 P/A + 2.76 OS Diversity + 2.33 Harvest	23.41	0.70	<0.001*
NonNative = 1.53 + 0.130 Area - 0.000883 Perimeter	8.57	0.34	0.001*
Native = 34.8 - 0.0423 P/A	18.17	0.37	<0.001*
Woody = 14.2 - 0.0154 P/A + 0.0730 Soil Moisture - 0.0815 Age + 4.08 OS Diversity - 0.400 1Km_Buffer	8.35	0.56	<0.001*
Herbaceous = - 11.4 + 0.00247 Perimeter + 0.263 Canopy Cover	8.42	0.34	0.001*

Table 5. Joint-plot vector fit analysis of environmental variables (1,000 permutations) within understory nonmetric multidimensional scaling (NMDS) ordination. OS = overstory.

Factor	NMDS1	NMDS2	R^2
Age	-0.89	-0.45	0.02
Area	-0.996	0.08	0.06
BA	-0.84	0.55	0.02
Canopy	-0.91	-0.41	0.20
FQI	-0.63	0.78	0.39
Harvest	-0.96	-0.29	0.01
meanC	-0.40	0.92	0.02
Moisture	0.51	0.86	0.16
OS Diversity	-0.79	0.61	0.19
OS Richness	-0.95	0.33	0.10
Perimeter	-0.89	-0.46	0.04
Perimeter.Area	0.93	-0.38	0.19

Table 6. Joint-plot vector fit analysis of environmental variables (1,000 permutations) within midstory nonmetric multidimensional scaling (NMDS) ordination. OS = overstory.

	NMDS1	**NMDS2**	**R^2**
1kmBuffer	0.50	-0.87	0.01
2kmBuffer	-0.61	0.79	0.07
Age	-0.71	0.70	0.08
Area	0.39	-0.92	0.02
BA	-0.93	-0.37	0.06
Canopy	-0.65	0.76	0.14
Distance	0.25	0.97	0.16
Diversity	0.92	0.38	0.07
Evenness	0.014	0.999	0.24
Moisture	0.99	-0.14	0.09
OS Richness	-0.10	-0.99	0.02
Perimeter	0.62	-0.78	0.05
Perimeter.Area	0.96	0.30	0.06
Richness	0.87	-0.49	0.08

Table 7. G-statistic with a Williams adjustment results for environmental factors relating to native species with high conservatism (>7 C) and low conservatism (<7 C). High factor cut-off was used after the top 10 ranked forests (33%). df = 1.

	Area (ha)	**Perimeter (m)**	**Perimeter/Area (m/ha)**	**Canopy Cover**	**Soil Moisture**
G_{adj}	3.11	1.05	2.50	0.04	2.31
p-value	0.08	0.31	0.32	0.84	0.13
	Forest Age	**Ave_Dist**	**2Km_Buffer**	**1Km_Buffer**	
Gadj	0.28	1.41	0.31	5.24	
p-value	0.59	0.24	0.58	0.02	

Table 8. G-statistic with a Williams adjustment results for ecological factors relating to native species with high conservatism (>7 C) and low conservatism (<7 C). High factor cut-off was used after the top 10 ranked forests (33%). df = 1.

	Basal Area	**Overstory Richness**	**Overstory Diversity**	**Harvest**
G_{adj}	0.37	5.75	6.02	1.59
p-value	0.54	0.02	0.01	0.21

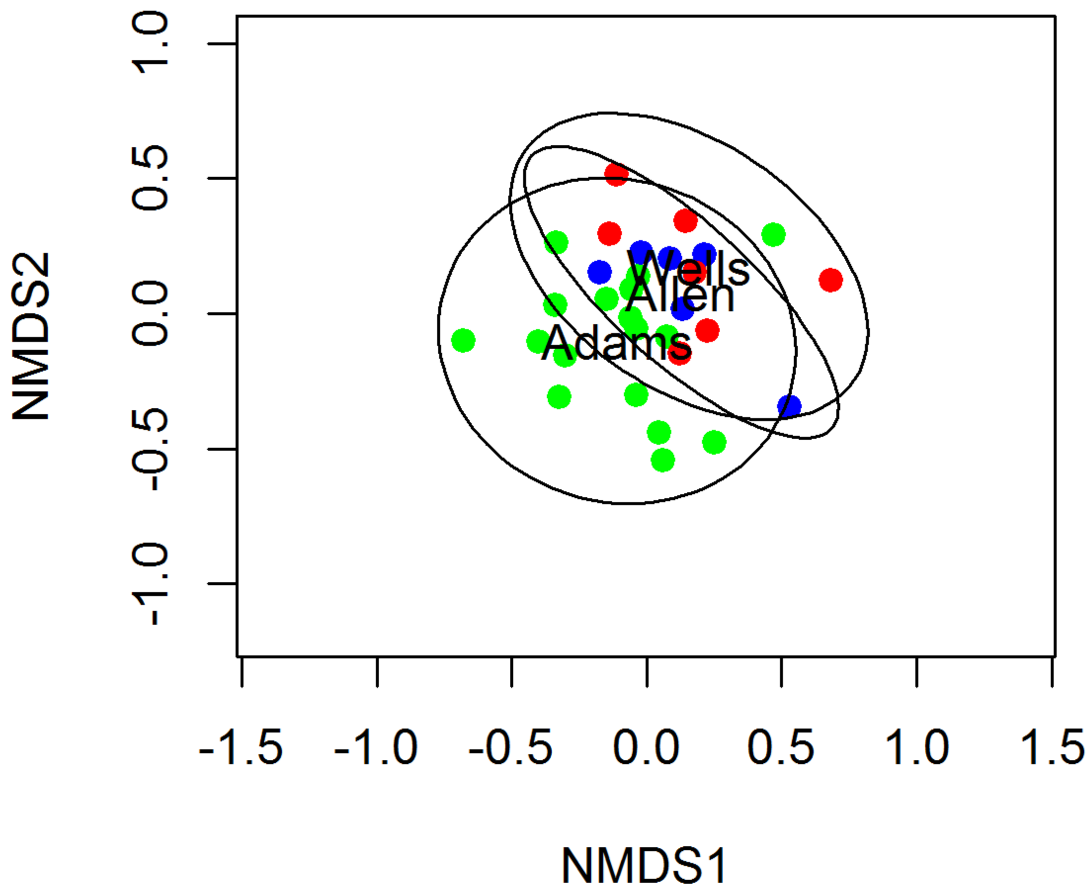

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination displaying site relationships of understory richness of Adams (green), Allen (blue), and Wells (red) Counties, IN with 95% confidence ellipses.

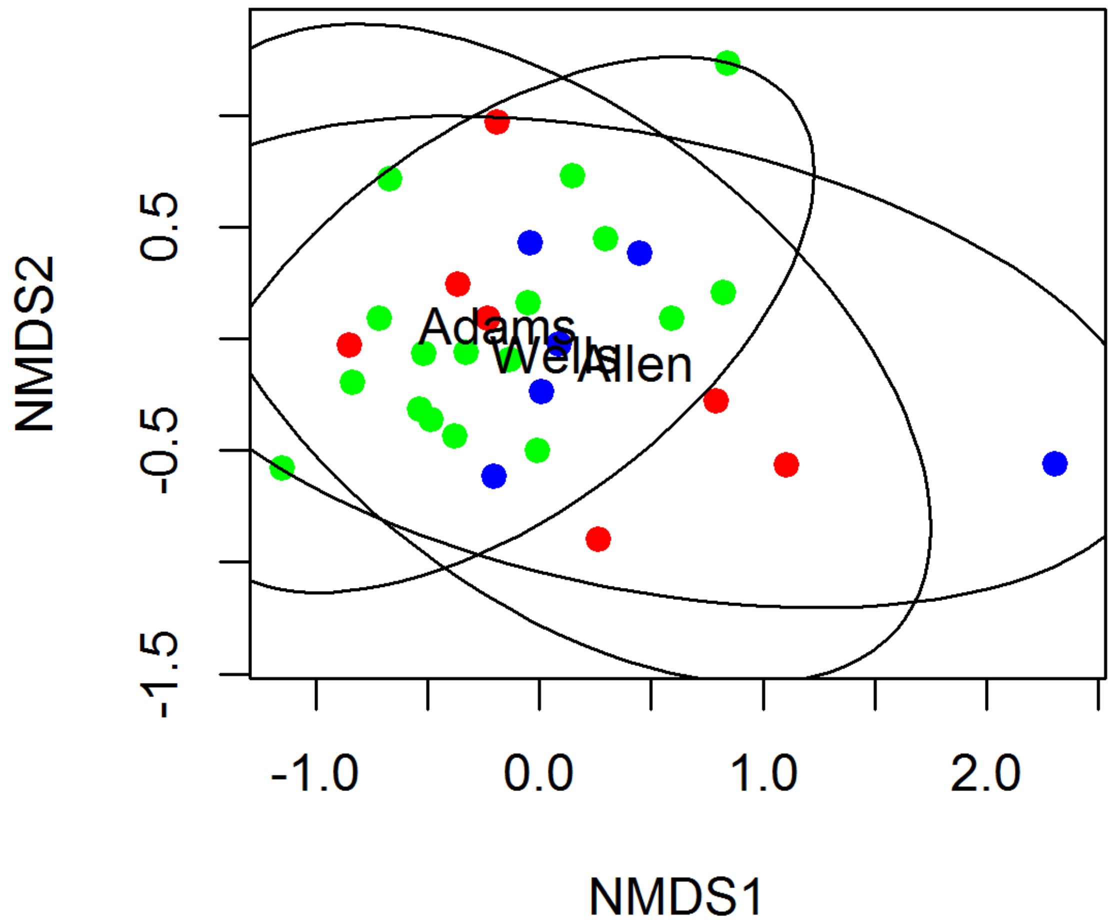

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination displaying site relationships of midstory richness of Adams (green), Allen (blue), and Wells (red) Counties, IN with 95% confidence ellipses.

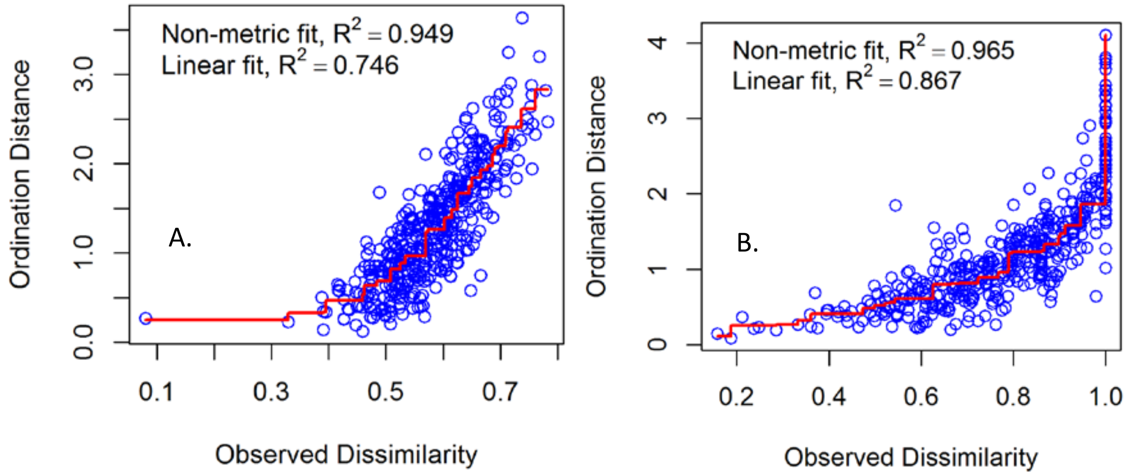

Figure 5. Stress plot for nonmetric multidimensional scaling (NMDS) ordination for understory (A) and midstory (B) species abundance.

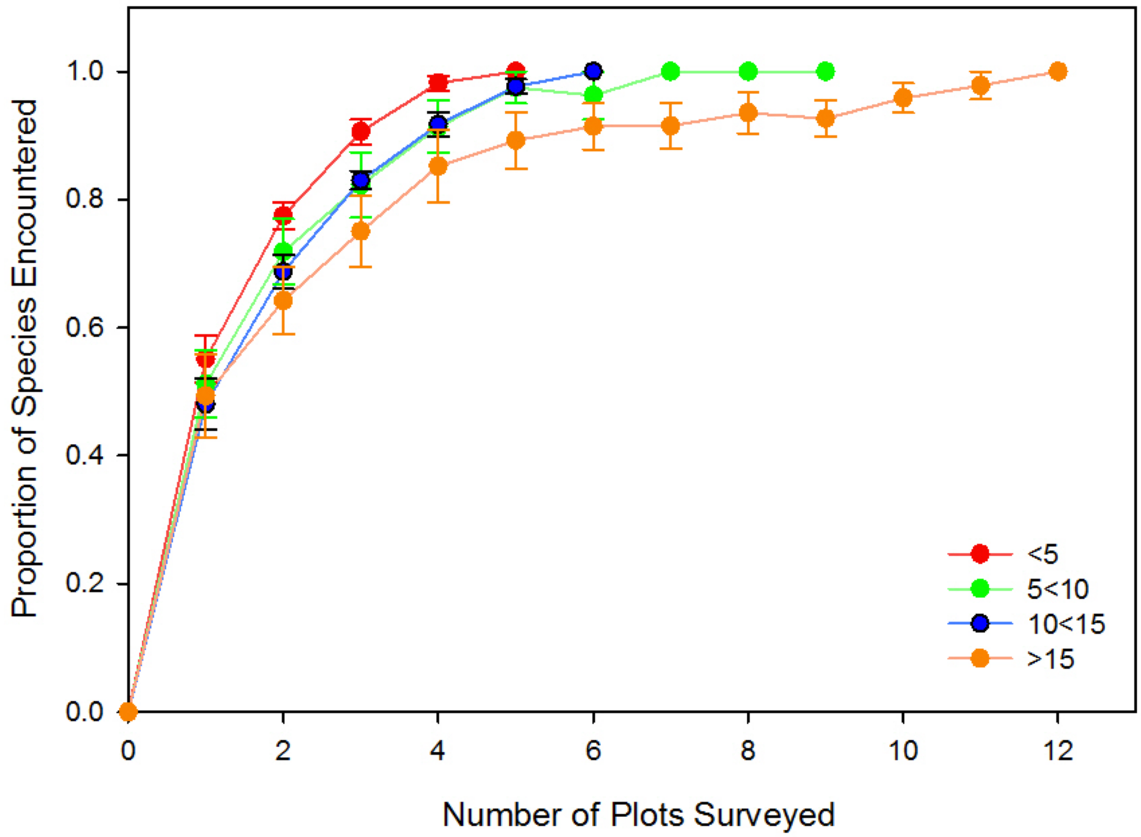

Figure 6. Species area curves for forest fragments displaying proportion of understory species encountered in size classes. Dip in 5<10 line was created by a bias of one forest having 9 plots while others having 4 or 5.

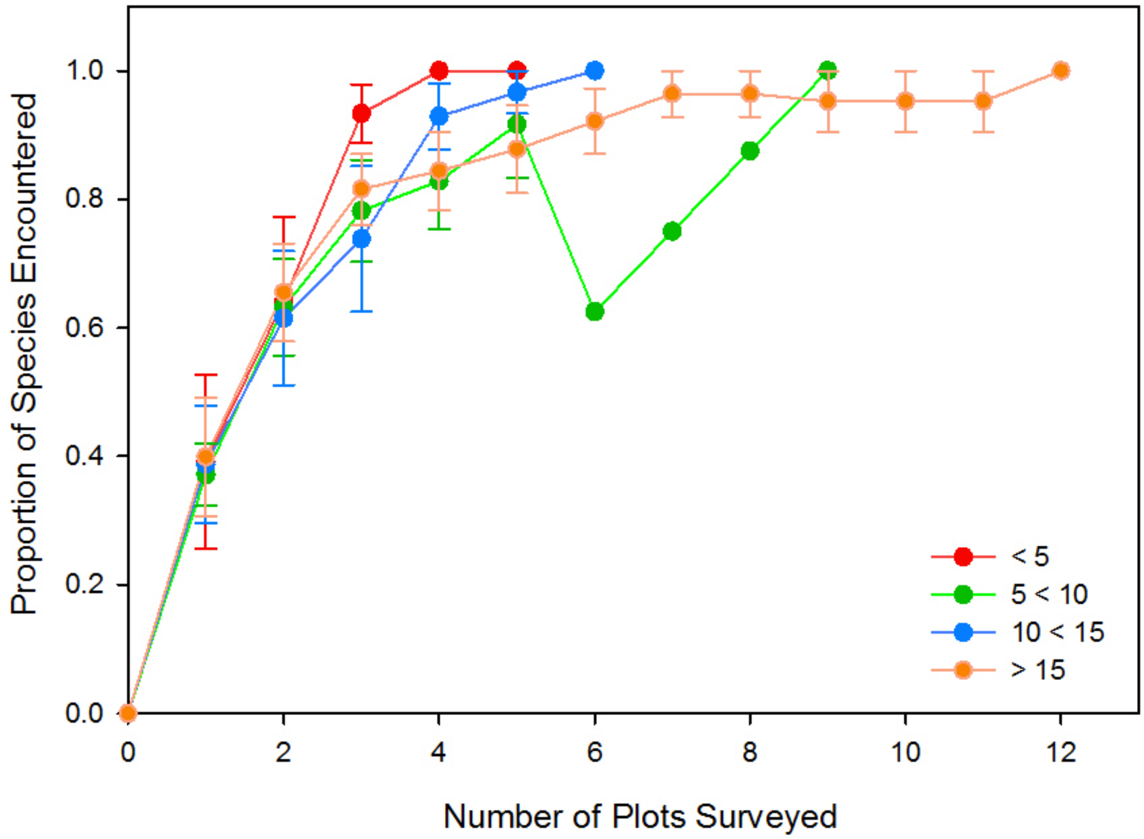

Figure 7. Species area curves for forest fragments displaying proportion of midstory species encountered in size classes. Dip in 5<10 line was created by a bias of one forest having 9 plots while others having 4 or 5.

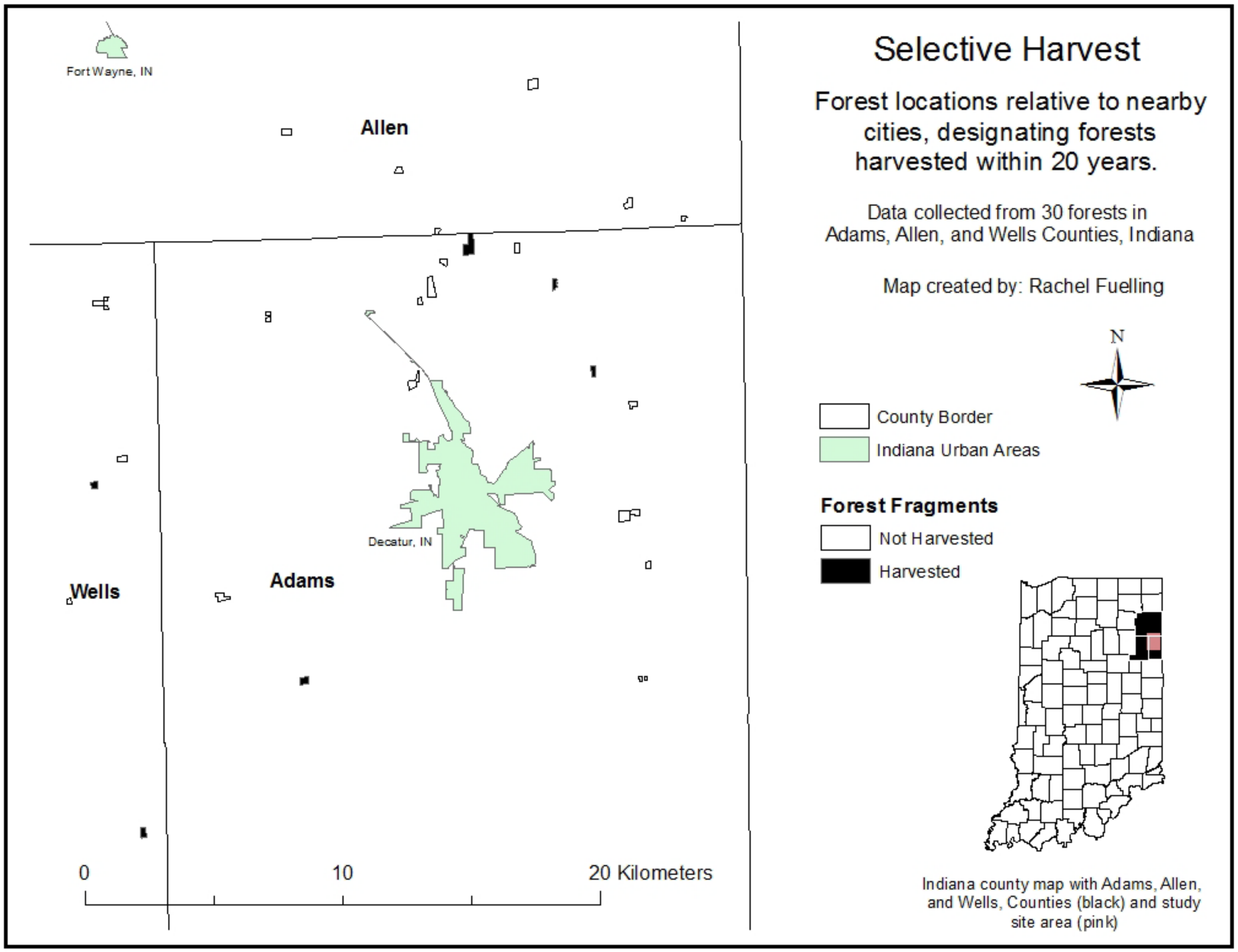

Figure 8. Map of forest locations relative to nearby cities (labeled) depicting harvested and not harvested forests within previous 20 years.

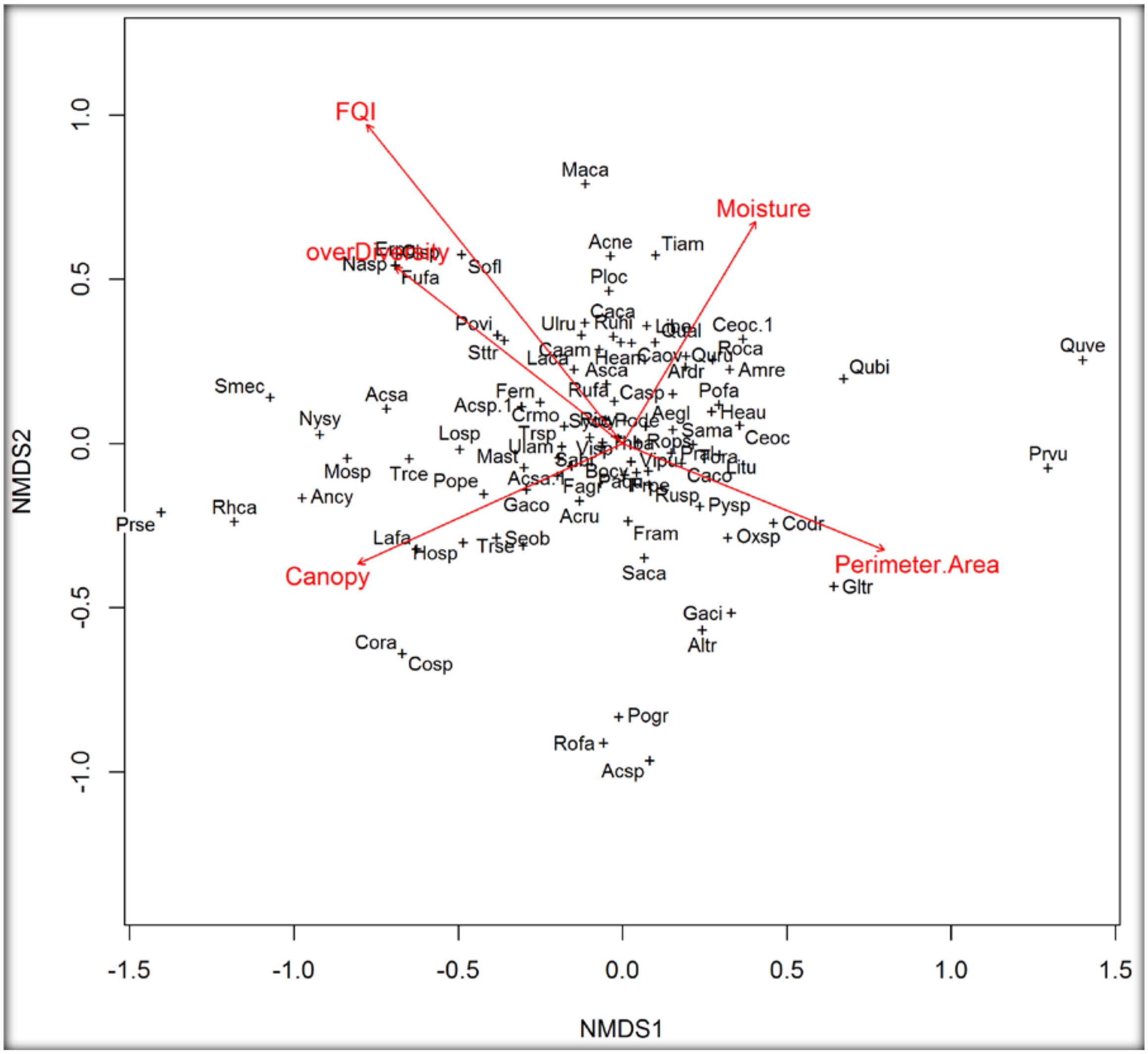

Figure 9. Nonmetric multidimensional scaling (NMDS) ordination of understory species abundance. Red joint plot vectors represent environmental variable influence on species distribution (cutoff R^2 for display = 0.2). Direction and length of vector relates to the influence of the factor on the species.

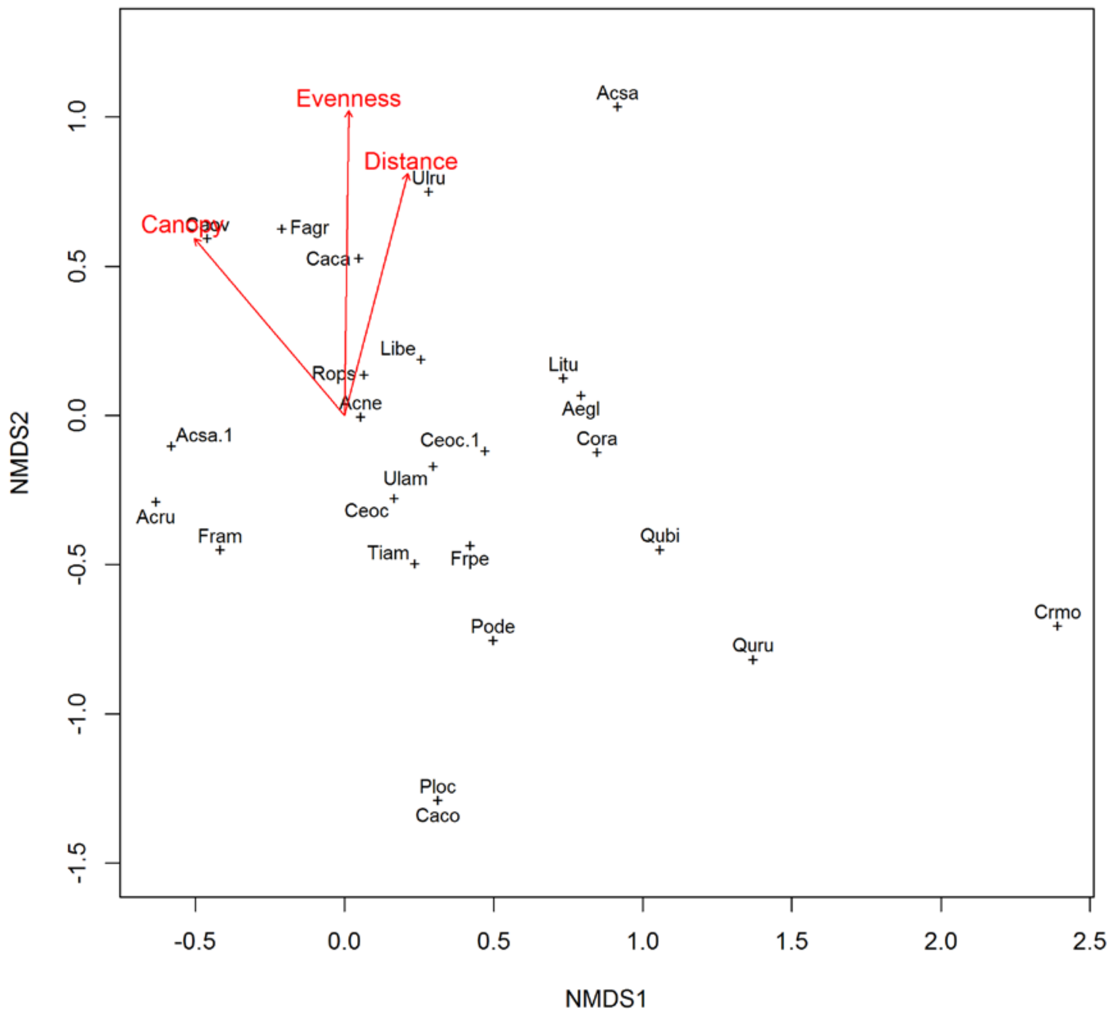

Figure 10. Nonmetric multidimensional scaling (NMDS) ordination of midstory species abundance. Red joint plot vectors represent environmental variable influence on species distribution (cutoff R^2 for display = 0.2). Direction and length of vector relates to the influence of the factor on the species.

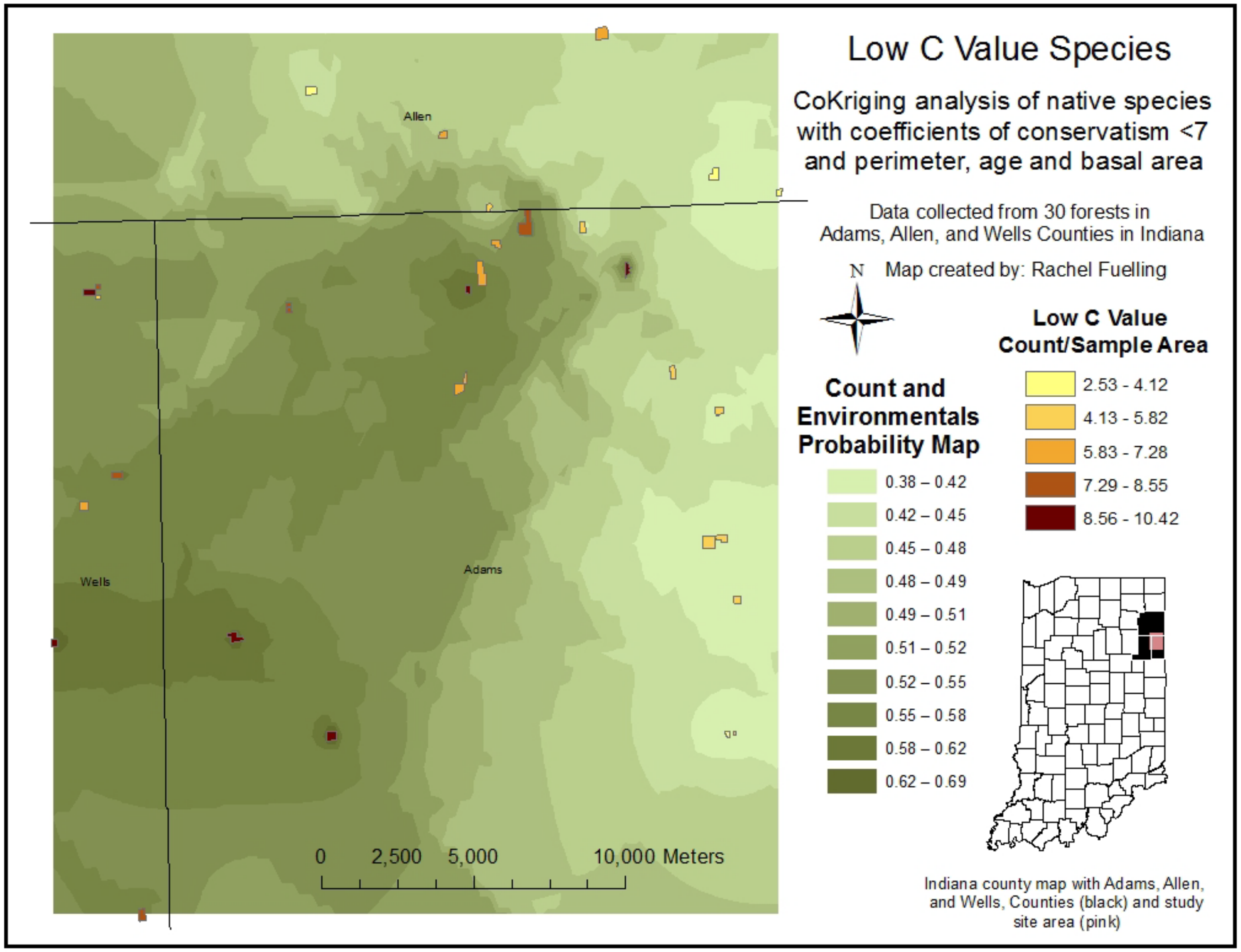

Figure 11. Map of forests fragments with individual plant count with low C values (<7)/ study area. CoKriging analysis performed using significant factors, including perimeter, age, and basal area and low C value count/ study area.

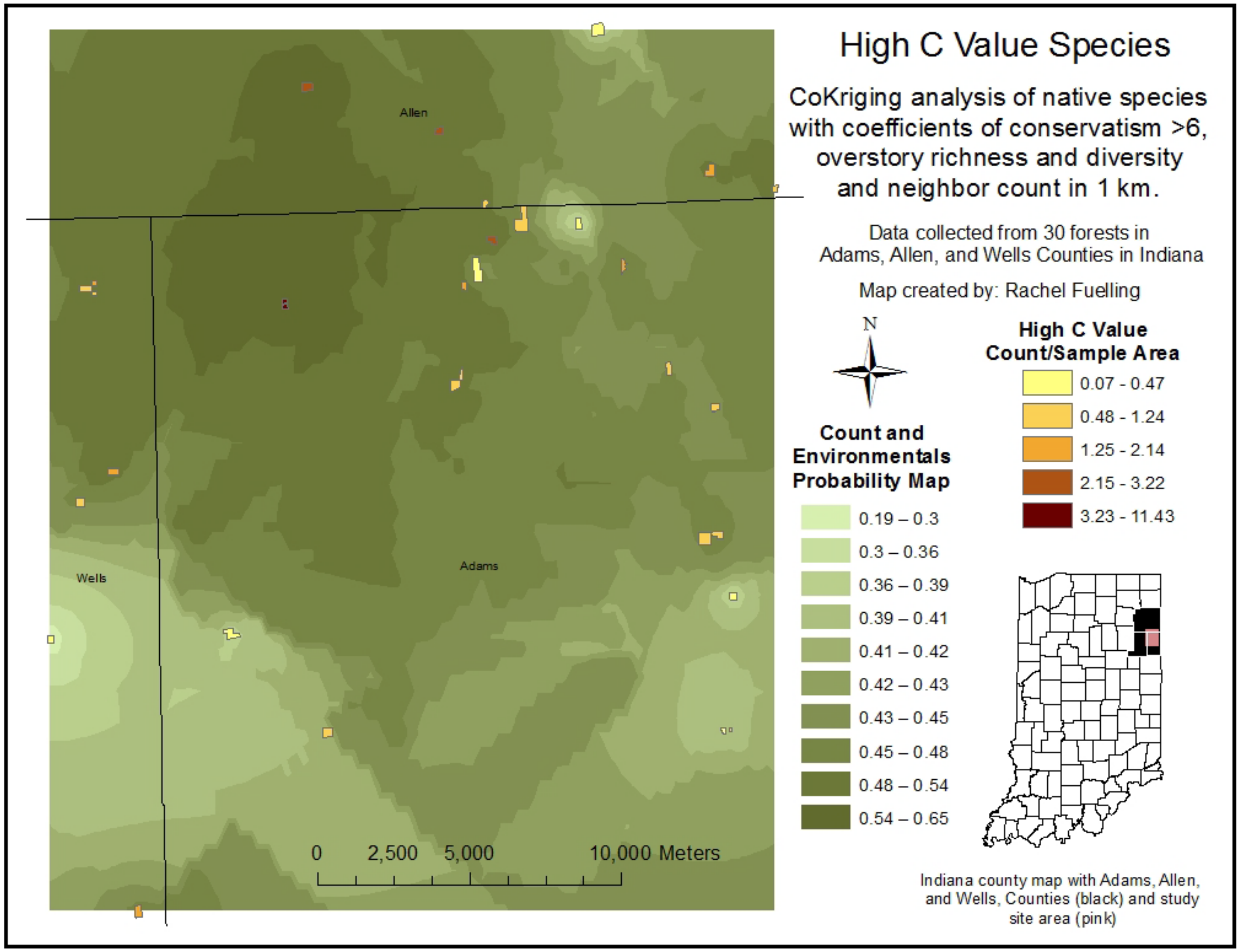

Figure 12. Map of forests fragments with individual plant count with high C values (≥7)/ study area. CoKriging analysis performed using significant G-analysis factors, including overstory richness, diversity and neighbor count in 1 km.

DISCUSSION

As ANOVA tests and NMDS analysis resulted in little difference between forests in different counties, analysis and observations were made at the forest level. Some difference between Adams and Wells Counties was described by the difference of canopy cover and number of forests within 2 km, but extensive overlap and similarity was seen between all three counties in direct comparison and ordination visualization. Thus, comparisons of forest factors to richness, diversity and conservatism of plant species was performed for northeast Indiana as a whole.

Forest Fragment Size and Shape

Fragment Area

Forest fragment area positively influenced understory richness and FQI, as well as midstory richness. Forest fragments in northeast Indiana show similar area-species-relationships as those noted with other island biogeography and fragmentation, thus they appear to follow the same principles (Ewers *et al.* 2007, Gonzalez *et al.* 2010, MacArthur and Wilson 1963, 1967). A diverse amount of habitats generally leads to an increase of inhabiting species, with more found in larger area fragments (Hannus and von Numers 2008, MacArthur and Wilson 1963, 1967, Stracey and Pimm 2009).

Forest Neighbors

The increase of niche space showed a greater relationship with increased diversity than isolation, of which distance and count of nearest neighbors was a surrogate. Distance to nearest neighbor had a negative effect with midstory species space. Neighbor count within 1 km radius showed negative relation with understory richness. When looking at native species' coefficients of conservatism in the understory, low valued species (<7) count doubled with a decrease in forest neighbor count in 1 km while high value species (≥7) had a 13% increase with more neighbors.

Previous studies noted a greater negative effect of isolation on species richness and diversity (MacArthur and Wilson 1963, 1967). An increase of richness is often noted with a decrease in distance of fragments as dispersal barriers are reduced or fragments are used as stepping stones for dispersal and could react more like one large forest (Aggemyr and Cousins 2012, MackArthur and Wilson 1963, 1967, Stracey and Pimm 2009). This isolation relationship was only noted with high C value plants, which increased with more neighbors in a 1 km radius. The lack of relationship with neighbors may the result of the agriculture matrix dividing the fragments. Dispersal is decreased over time as the dispersible propagules are changed when diaspores are lost in uninhabitable terrain (Cody and Overton 1996, Oliverieri and Gouyon 1985). As agricultural land is highly cultivated, continuously disturbed, and treated with herbicides with the intent to create a crop monoculture, loss of propagules through dispersal should be great, pushing for a genetic trend for short dispersal patterns. Short dispersal patterns are also noted in more stable landscapes and non-harvested, aging forests are considered stable (Talavera *et al.* 2012).

Fragment Perimeter

Understory species space and midstory diversity and FQI were negatively associated with perimeter:area ratio. The edge effect of the agriculture matrix is a deterrent to plant richness. The maintenance of crops purposefully excludes all undesired growth. Administering herbicide reduces dispersal and may cause run off that reduces habitable space and kills susceptible individuals or species, planting a monoculture reduces niches, and constant plowing creates high disturbance levels. This maintenance of the agriculture matrix influences the environment of the adjacent forest, creating an edge, which shows species richness values of a different habitat from the deeper woods (Gonzalez *et al.* 2010).

Agriculture landscape not only provides an effective border, but involves a great contrast of plant diversity and height from the forest fragment. The edge effect created by the agriculture matrix was greater on smaller fragments as the ratio of forest edge to area is increased (Ewers *et al.* 2007, Gonzalez *et al.* 2010). In addition, the shape of the fragment, no matter its area, played a role with the perimeter:area ratio. As there is great and abrupt contrast in vegetation density between the forest and agriculture landscape, the edge would have great negative effect (Ries *et al.* 2004).

Non-native species count increased with forest area and decrease with forest perimeter. Non-native recruitment is generally described as greater with smaller fragments and forests with greater edge to area ratio and with forest fragments in human-modified landscapes (Borgmann and Rodewald 2005, Bruna 2002, With 2002). This was not noted in this study, but the edge effect was accounted for by leaving a 25.6 m border. As the edge and the interior may be considered different environments with the edge having a greater increase in richness, the influx of non-native species could have been found here (Gonzalez *et al.* 2010).

Native species, which accounted for 91% of identified species, was negatively related to the forest perimeter:area ratio. Woody species also decreased with an increase of the forest: perimeter ratio. The decrease in species count is relatable to the negative effect of the edge.

Understory diversity and herbaceous species count significantly increased with forest perimeter. This relationship may have increased without the 25.6 m buffer used as species richness is influenced by perimeter, with greater counts found near the edge (Gonzalez *et al.* 2010). This is primarily due to the increase of light with the thinner canopy, but also through dispersal patterns, with dispersal by wind and animals having higher counts in the edge (Gonzalez *et al.* 2010). This relationship, however, does not negate the need for an interior zone for specialist species, such as shade obligatory species.

Intermediate Disturbance

Intermediate disturbance is produced by selective harvest of the overstory, which had a direct influence with midstory richness and FQI values. This follows literature, which shows highest richness following mid-level disturbance events (Connell 1978, Dial and Roughgarden 1998, Townsend *et al.* 1997). This level of disturbance balances superior competitors and those more tolerable to disturbance (Collins 1995). Intermediate disturbance altered forest age, overstory diversity, and canopy cover, each of which had direct influence on under and midstory richness and diversity.

Forest age was negatively associated with understory diversity and woody species count. This coincides with younger forests having greater richness with a balance of competitors (Collins 1995). An increase of non-native species count was associated with older forests. Intermediate disturbance, created by selective harvest, alters succession pathways, which would normally be dominated by high competitor species in the climax stage (Martin and Gower 1996). Large hardwood trees, such as oak and elm, are commonly removed as high value trees. These trees are characteristic of a mature forest in later succession stages. With their removal, ash, maple, and hawthorn dominate, resulting in greater diversity of each forest level as competition is more balanced with species, such as natives, that are more disturbance tolerant (Collins 1995).

Overstory diversity had positive relationship with understory richness, FQI, and understory species space. Overstory diversity positively influenced midstory richness, diversity, and FQI. Woody species count also increase with an increase of overstory diversity. Levels of conservatism (high and low C values) were affected, with overstory richness and diversity negatively influencing low valued species. Overstory richness positively influenced high value species. Overstory diversity is directly influenced by the removal of high value trees generally found in later succession forests, promoting younger forests, which have greater richness values. Interactions between species in the over and understory influence canopy composition (Quigley and Platt 1996). Understory composition influences the spatial pattern of the overstory trees through survival and growth of juvenile trees in gap areas (Platt and Schwartz 1990). More overstory diversity provides several environment types for under and mid story species. With several niches to fill, the competition between understory species decreases, allowing for the greater diversity seen.

The intermediate disturbance caused by selective harvest may also promoted spread of seeds as unpredictable environments select for polymorphism for increase advantages in dispersal distance (Snyder 2011). Although seed weight or dispersal type was not directly measured, spread likely would have increased richness in the understory and some species would eventually lead to vertical succession and enter into the canopy.

Canopy cover positively influenced understory diversity and the distribution of understory and midstory species relative to each other. An increase of canopy cover also related to an increase of herbaceous species count. The change in canopy is directly influenced by the selective harvests of trees as it constantly shifts between open and close, providing areas for shade-tolerant and obligate plants as well as shade-intolerant. This opening is important for vertical success of one strata to the next as light availability promotes growth.

Forest Fragments

Each of the forest fragments studied displayed species-area curves (Figures 6,7), thus each could be managed similarly, despite size. Small fragments may lack forest like conditions to maintain all species as they are entirely composed of edge habitat (Ewers *et al.* 2007). This was not the case in the studied forest fragments, which had areas ranging from 1.5-33.5 hectares. Thus, forest fragments falling within this range could possibly be managed as a single forest ecosystem.

Understanding how to manage these forests and what size needs to be managed is important to eastern United States as young forests have shown a decline due to the lack of management on privately owned land (Trani *et al.* 2001). Management, particularly through intermediate disturbance, would increase the current distribution of young forests, which is below what is needed to increase biodiversity (Askins 2001).

CONCLUSIONS

Forests of Northeast Indiana are relatively small and isolated with no large forest mainland to effectively act as a species source. Thus, fragmentation studies incorporating forest size, shape, age, and structure are important to understand plant diversity and distribution.

Relationships between forest fragment and factors were analyzed with differences in diversity chiefly arising from perimeter:area ratio and selective harvests, with little to no relationship with number or distance of neighbor forests. Large forest fragments that are selectively harvested with some edge effect show the greatest amount of plant diversity. The results of this study are similar to other research done on forest fragments and island biogeography in regards to size and disturbance. Isolation showed markedly different results in this study than previous works. By comparing the literature review to this study's results, it is shown that fragmentation principles are applicable to forest patches surrounded by an agriculture matrix in northeast Indiana.

Future research of species distribution related to seed size, dispersal mechanisms and soil types will be conducted as an additional analysis. This data will be derived by counts and identified species from this study. Further research can also include comparisons within the community. Bacteria, insects, reptiles, mammals, and amphibians could be identified within the studied forests for community analysis to ascertain if plant diversity is a contributing factor to another guild's diversity or richness.

Future research of forest fragments in northeast Indiana should include diversity studies with forests undergoing management. In the thirty forests studied, six forest fragments were selectively harvested within the previous 20 years. Two additional forests came under management by a forest products company just before the study. Companies such as this perform selective harvests and own other forests that were in the study. As selective harvesting related directly with diversity and influenced forest age, canopy cover, and overstory diversity, changes in these factors could be detailed with newly managed forests.

Additional research should be conducted with forest fragments smaller than 1.5 ha, the smallest fragment used in this study, to establish what is a stand of trees versus a forest ecosystem. Management policies may change with the smaller forests, which would be composed of edge environment. This could define what makes a true forest as the diversity of plant and animal species should change.

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APPENDICES

Appendix A
Multiple Regression Analysis

A. Understory Richness

Predictor	Coef	SE Coef	T	P
Constant	4.507	5.347	2.71	0.011
Area (ha)	0.41024	0.09031	4.54	0.000
Overstory Diversity	8.737	2.797	3.12	0.004

B. Understory Shannon Index

Predictor	Coef	SE Coef	T	P
Constant	0.5595	0.7360	0.76	0.454
Perimeter (m)	0.00021705	0.00005202	4.17	0.000
Canopy Cover	0.025950	0.008225	3.16	0.004
Forest Age	-0.009656	0.004259	-2.27	0.032
1Km_Buffer	-0.05783	0.02144	-2.70	0.012

C. Understory FQI

Predictor	Coef	SE Coef	T	P
Constant	12.890	2.795	4.61	0.000
Area (ha)	0.15172	0.04720	3.21	0.003
Overstory Diversity	4.179	1.462	2.86	0.008

D. Midstory Richness

Predictor	Coef	SE Coef	T	P
Constant	-2.470	2.305	-1.07	0.295
Area (ha)	0.37608	0.07741	4.86	0.000
Perimeter (m)	-0.0023487	0.0007200	-3.26	0.003
Soil Moisture	0.04929	0.01974	2.50	0.020
Overstory Diversity	2.597	1.025	2.53	0.018
Harvest	2.8036	0.7246	3.87	0.001

E. Midstory Shannon Index

Predictor	Coef	SE Coef	T	P
Constant	0.3794	0.6313	0.60	0.553
Perimeter/Area	-0.0038356	0.0009884	-3.88	0.001
Soil Moisture	0.008836	0.004279	2.06	0.049
Overstory Diversity	0.5844	0.2457	2.38	0.025

F. Midstory FQI

Predictor	Coef	SE Coef	T	P
Constant	8.538	2.891	2.95	0.007
Perimeter/Area	-0.029274	0.004965	-5.90	0.000
Overstory Diversity	2.758	1.300	2.12	0.044
Harvest	2.3338	0.8772	2.66	0.013

G. Non-native Species

Predictor	Coef	SE Coef	T	P
Constant	1.5288	0.3131	4.88	0.000
Area (ha)	0.12968	0.03439	3.77	0.001
Perimeter (m)	-0.0008829	0.0003446	-2.56	0.016

H. Native Species

Predictor	Coef	SE Coef	T	P
Constant	34.800	1.894	18.38	0.000
Perimeter/Area	-0.042328	0.009929	-4.26	0.000

I. Woody Species

Predictor	Coef	SE Coef	T	P
Constant	14.210	4.277	3.32	0.003
Perimeter/Area	-0.015360	0.005808	-2.64	0.014
Soil Moisture	0.07303	0.02577	2.83	0.009
Forest Age	-0.08146	0.03605	-2.26	0.033
Overstory Diversity	4.077	1.458	2.80	0.010
1Km_Buffer	-0.4000	0.1875	-2.13	0.043

J. Herbaceous Species

Predictor	Coef	SE Coef	T	P
Constant	-11.358	9.792	-1.16	0.256
Perimeter (m)	0.0024674	0.0006906	3.57	0.001
Canopy Cover	0.2626	0.1060	2.48	0.020

K. Native Species with C <7

Predictor	Coef	SE Coef	T	P
Constant	7.201	1.431	5.03	0.000
Perimeter (m)	0.0009925	0.0003931	2.52	0.018
Forest Age	-0.07404	0.03266	-2.27	0.032
Basal Area	0.03855	0.01638	2.35	0.026

Appendix B

ANOVA Tables for Multiple Regression

A. Understory Richness

Source	DF	SS	MS	F	P
Regression	2	627.62	313.81	17.07	0.000
Residual Error	27	496.24	18.38		
Total	29	1123.87			

B. Understory Shannon Index

Source	DF	SS	MS	F	P
Regression	5	1.82652	0.36530	7.53	0.000
Residual Error	24	1.16467	0.04853		
Total	29	2.99119			

C. Understory FQI

Source	DF	SS	MS	F	P
Regression	2	105.030	52.515	10.46	0.000
Residual Error	27	135.584	5.022		
Total	29	240.613			

D. Midstory Richness

Source	DF	SS	MS	F	P
Regression	5	259.073	51.815	22.90	0.000
Residual Error	24	54.294	2.262		
Total	29	313.367			

E. Midstory Shannon Index

Source	DF	SS	MS	F	P
Regression	3	5.6297	1.8766	15.09	0.000
Residual Error	26	3.2332	0.1244		
Total	29	8.8630			

F. Midstory FQI

Source	DF	SS	MS	F	P
Regression	3	249.243	83.081	23.41	0.000
Residual Error	26	92.264	3.549		
Total	29	341.507			

G. Non-Native Species

Source	DF	SS	MS	F	P
Regression	2	9.7879	4.8939	8.57	0.001
Residual Error	27	15.4121	0.5708		
Total	29	25.2000			

H. Native Species

Source	DF	SS	MS	F	P
Regression	1	297.95	297.95	18.17	0.000
Residual Error	28	459.02	16.39		
Total	29	756.97			

I. Woody Species

Source	DF	SS	MS	F	P
Regression	5	174.381	34.876	8.35	0.000
Residual Error	24	100.286	4.179		
Total	29	274.667			

J. Herbaceous Species

Source	DF	SS	MS	F	P
Regression	2	179.46	89.73	8.42	0.001
Residual Error	27	287.74	10.66		
Total	29	467.20			

K. Native Species with C <7

Source	DF	SS	MS	F	P
Regression	3	49.502	16.501	4.84	0.008
Residual Error	26	88.633	3.409		
Total	29	138.135			

Appendix C
Annotated Species List

Annotated species list for understory surveys in Adams, Allen, Wells Counties forests (n = 17, 6, 7, respectively). Species binomial followed by county code (AD=Adams, AL=Allen, W=Wells) – mean number of individuals (standard error).

ACERACEAE

Acer negundo L.: AD – 6.17(5.15); AL – 1.33(4.29); W – 4.43(2.72)

Acer rubrum L.: AD – 2.47(1.62); AL – 2.86(2.86)

Acer saccharinum L.: AD – 0.76(.58)

Acer saccharum Marshall: AD – 93.59(28.22); AL – 32.33(12.77); W – 35.29(19.62)

Acer spp.: AD – 5.17(3.29)

Acer spicatum L.: AD – 0.94(.094)

ALISMATACEAE

Sagittaria brevirostra Mack.: AD – 9.35(2.89); AL – 4.67(1.82); W – 20.71(12.28)

AMARANTHACEAE

Amaranthus retroflexus L.: AD – 2 2.41(9.44); AL – 21.33(11.70); W – 63.71(34.08)

AMARYLLIDACEAE

Allium tricoccum Aiton: AD – 4.35(3.01); AL – 0.83(0.83); W – 3.14(2.21)

ANACARDIACEAE

Toxicodendron radicans L.: AD – 76.18(21.55); AL – 460.83(347.88); W – 145.71(61.25)

APIACEAE

Sanicula marilandica L.: AD – 327.41(79.07); AL – 254.33(63.68); W – 367.14(126.99)

Thaspium barbinode Michx.: AD – 22.53(9.66); AL – 20.17(11.91); W – 8.00(3.19)

ARACEAE

Arisaema dracontium L.: AD – 0.18(0.18); W – 1.29(1.29)

ARISTOLOCHIACEAE

Asarum canadense L.: AD – 195.35(58.39); AL – 75.33(73.74); W – 224.14(106.53)

ASTERACEAE

Cichorium sp.: AD – 0.18(0.18)

Erigeron pulchellus Michx.: AD – 0.88(0.88)

Helenium autumnale L.: AD – 15.47(7.28); AL – 42.67(27.33); W - 62.00(47.42)

Prenanthes altissima L.: AD – 16.12(4.90); AL – 9.33(3.98); W – 16.71(6.50)

Rudbeckia hirta L.: AD – 2.41(1.29); AL – 22.33(19.59); W – 4.57(3.02)

Senecio obovatus Muhl.: AD – 3.59(2.92); W – 0.43(0.43)

Solidago flexicaulis L.: AD – 12.06(12.06); W – 8.00(8.00)

Symphyotrichum cordifolium L.: AD – 5.35(2.53); AL – 5.17(5.17); W – 1014(0.63)

BERBERIDACEAE

Podophyllum peltatum L.: AD – 34.94(18.28); AL – 4.83(4.06)

BETULACEAE

Carpinus caroliniana Walter.: AD – 4.71(2.16); AL – 9.00(3.82); W – 5.43(2.92)

CAMPANULACEAE

Campanula americana L.: AD – 0.29(0.29)

Lobelia sphilitica L.: AD – 0.65(0.45); W – 2.43(2.43)

CORNACEAE

Cornus drummondii C.A. Mey.: AD – 0.82(0.46)

Cornus racemosa Lam.: AD – 1.88(1.88)

Cornus sp.: AD – 0.29(0.29)

Nyssa sylvatica Marshall: AD – 2.12(1.46)

CYPERACEAE

Carex sp.: AD – 58.47(43.68); AL – 15.67(5.60); W – 52.71(29.66)

FABACEAE

Gleditisia tricanthos L.: AD – 0.29(0.17); AL – 5.00(5.00); W – 0.86(0.86)

Robinia pseudoacacia Ashe: AD – 7.76(4.12); AL – 7.17(4.32); W – 15.71(8.33)

FAGACEAE

Fagus grandifolia Ehrh.: AD – 3.29(1.09); AL – 0.67(0.49); W – 0.86(0.70)

Quercus alba L.: AD – 1.53(1.07); AL – 2.50(1.43); W – 1.00(0.58)

Quercus bicolor Willd.: AD – 0.94(0.82); AL – 2.50(1.96); W – 19.14(13.86)

Quercus rubra L.: AD – 1.12(0.45); AL – 1.50(0.96); W – 1.29(0.42)

Quercus velutina Lam.: W – 0.86(0.86)

FUMARIACEAE

Fumariaceae family: AD – 0.29(0.29)

GROSSULARIACEAE

Ribes cynosbati L.: AD – 24.29(7.40); AL – 11.00(5.93); W – 59.86(19.86)

HIPPOCASANACEAE

Aesculus glabra Willd.: AD – 0.76(0.53); AL – 0.17(0.17); W – 3.14(2.82)

JUGLANDACEAE

Carya cordiformis Wangenh.: AD – 8.12(1.45); AL – 16.17(5.08); W – 33.71(14.54)

Carya ovata Mill.: AD – 10.41(5.91); AL – 13.33(5.43); W – 11.43(6.25)

LAMIACEAE

Monarda sp.: AD – 4.65(2.34)

Prunella vulgaris L.: AL – 0.33(0.33); W – 2.57(2.57)

LAURACEAE

Lindera benzoin L.: AD – 27.06(14.24); AL – 43.50(24.03); W – 34.43(12.59)

LILIACEAE

Maianthemum canadense Desf.: AL – 4.50(4.30); W – 31.43(20.62)

Mianthemum stellatum L.: AD – 86.65(25.07); AL – 12.33(7.01); W – 20.43(11.52)

Narcissus sp.: AD – 1.24(1.24)

Trillium cernuum L.: AD – 6.47(4.39)

Trillium sessile L.: AD – 8.71(5.27); AL – 0.17(0.17); W – 0.57(0.57)

Trillium sp.: AD – 10.94(2.86); AL – 4.33(1.74); W – 4.14(3.22)

MAGNOLIACEAE

Liriodendron tulipifera L.: AD – 0.06(0.036); W – 1.00(1.00)

OLEACEAE

Fraxinus americana L.: AD – 46.76(8.09); AL – 17.00(5.08); W – 43.43(30.71)

Fraxinus pennsylvanica Marshall: AD – 40.00(12.95); AL – 47.17(20.86); W – 68.14(46.72)

OXALIDACEAE

Oxalis sp. AD – 1.65(0.82); AL – 5.50(4.75); W – 5.29(4.79)

PAPAVERACEAE

Sanguinaria Canadensis L.: AD – 3.59(1.40); AL – 0.17(0.17); W – 1.14(0.59)

PLANTANACEAE

Platanus occidentalis L.: AL – 0.50(0.50)

POACEAE

Species: AD – 178.53(84.61); AL – 149.83(42.22); W – 191.57(102.08)

POLYGONACEAE

Polygonum virginianum L.: AD – 0.71(0.37); AL – 0.33(0.33); W – 2.14(1.49)

PYROLACEAE

Pyrola sp.: AD – 37.24(19.36); AL – 33.33(11.57); W – 60.00(43.24)

RANUNCULACEAE

Anemone cylindrical A. Gray: AD – 4.41(3.60)

RHAMNACEAE

Rhamnus cathartica L.: AD – 2.65(2.28)

ROSACEAE

Species: AD – 2.12(1.36)

Crataegus mollis Scheele: AD – 2.18(1.37); AL – 0.50(0.50); W – 1.14(0.83)

Prunus serotina Ehrh.: AD – 0.06(0.06)

Rosa carolina L.: AD – 3.18(1.57); AL – 4.67(3.53); W – 38.29(17.78)

Rubus sp.: AD – 18.76(6.68); AL – 27.83(11.99); W – 26.86(9.99)

RUBIACEAE

Species: AD – 165.00(38.77); AL – 213.83(93.97); W – 146.57(54.98)

Cephalanthus occidentalis L.: AD – 6.35(2.72); AL – 18.00(6.63); W – 48.86(26.20)

Gallium circaezans Michx.: AD – 11.94(6.06); AL – 13.33(8.63); W – 13.86(9.44)

Galium concinnum Torr.: AD – 16.65(9.29); W – 62.43(40.30)

Houstonia sp.: AD – 8.35(5.53); W – 1.57(1.27)

SALICACEAE

Populous deltoids W.: AD – 1.29(0.65); AL – 0.50(0.50); W – 1.57(1.27)

Populus grandidentata Michx.: AD – 0.12(0.08)

SAXIFAGACEAE

Heuchera americana L. AD – 84.53(77.74); AL – 141(67.77); W – 1.29(1.13)

SMILACACEAE

Smilax ecirrhata Emgel.: AD – 0.29(0.24)

STAPHYLEACEAE

Staphylea trifolia L.: AL – 4.67(4.67)

TILIACEAE

Tilia americana L.: AD – 0.12(0.12); AL – 1.00(0.82); W – 0.71(0.57)

ULMACEAE

Celtis occidentalis L.: W – 0.57(0.57)

Ulmus americana L.: AD – 9.12(2.88); AL – 4.00(2.44); W – 2.43(1.11)

Ulmus rubra Muhl.: AD – 6.82(2.33); AL – 3.33(2.12); W – 10.57(3.99)

URTICACEAE

Boehmeria cylindrica L.: AD – 80.53(18.00); AL – 33.00(10.44); W – 102.71(50.48)

Laportea Canadensis L.: AD – 31.47(20.09); AL – 76.00(43.11); W – 0.57(0.57)

VIOLACEAE

Viola pubescens Aiton: AD – 67.94(25.55)17; AL – 34.00(13.61); W – 72.71(47.58)

VITACEAE

Parthenocissus quinquefolia L.: AD – 199.12(27.21); AL – 125.83(28.15); W - 170.86(52.98)

Vitis sp.: AD – 18.41(5.57); AL – 143.00(131.25); W – 58.29(46.51)

Appendix D
Annotated Species List

Annotated species list for midstory surveys in Adams, Allen, Wells Counties forests (n = 17, 6, 7, respectively). Species binomial followed by county code (AD=Adams, AL=Allen, W=Wells) – mean number of individuals (standard error).

ACERACEAE

Acer negundo L.: AD – 0.24(0.18)

Acer rebrum L.: AD – 4.0(1.18); AL – 4.5(1.16); W – 3.43(1.02)

Acer saccharinum L.: AD – 1.00(0.61)

Acer saccharum Marshall.: AD – 9.24(2.39); AL – 6.33(1.07); W – 6.86(1.72)

BETULACEAE

Carpinus caroliniana Walter.: AD – 1.59(0.63); AL – 3.50(0.90); W – 2.0(0.61)

CORNACEAE

Cornus racemosa Lam.: AD – 0.27(0.24); W – 0.14(0.09)

FABACEAE

Robinia pseudoacacia Ashe.: AD – 1.18(0.64); AL – 1.00(0.49); AL – 0.43(0.28)

FAGACEAE

Fagus grandifolia Ehrh.: AD 2.53(0.81); AL – 0.83(0.32)

Quercus rubra L.: W – 0.14(0.09)

Quercus bicolor Willd.: AD – 0.06(0.06); W – 0.29(0.12)

HIPPOCASTANACEAE

Aesculus glabra Willd.: AD – 0.35(0.26); W – 0.86(0.29)

JUGLANDACEAE

Carya cordiformis Wangenh.: W – 0.29(0.18)

Carya ovata Mill.: AD – 0.71(0.53); AL – 0.17(0.10); W – 1.29(0.72)

LAURACEAE

Lindera benzoin L.: AD – 0.24(0.18)

MAGNOLIACEAE

Liriodendron tulipifera L.: AD – 0.06(0.06)

OLEACEAE

Fraxinus pennsylvanica Marshall: AD – 0.35(0.24); AL – 1.33(0.42); W – 3.43(1.65)

Fraxinas americana L.: AD – 1.06(0.33)

PLATANACEAE

Platanus occidentalis L.: W – 0.43(0.28)

ROSACEAE

Crataegus mollis Schelle: AD – 0.24(0.14); AL – 0.50(0.20); W – 1.57(0.91)

RUBIACEAE

Cephalanthus occidentalis L.: AL – 1.50(0.57); 0.29(0.18)

SALICACEAE

Populus deltoids W.: AD – 0.06(0.06); W – 0.14(0.09)

TILIACEAE

Tilia americana L.: AD – 0.82(0.56); AL – 0.83(0.39); W – 0.43(0.28)

ULMACEAE

Ulmus americana L.: AD – 1.82(0.54); AL – 1.33(0.37); W – 4.57(1.56)

Celtis occidentalis L.: AL – 0.17(0.10); W – 0.14(0.09)

Ulmus rubra Muhl.: AD – 0.325(0.17); 0.33(0.13); 0.29(0.12)